UNIVERSIDADE FEDERAL DO ESPÍRITO SANTO
CENTRO DE CIÊNCIAS HUMANAS E NATURAIS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

Sistemática de Bethylinae (Hymenoptera, Bethylidae)

Magno Suprani Ramos

Vitória, ES
Fevereiro, 2017

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Magno Suprani Ramos

Orientador: Celso Oliveira Azevedo

Tese submetida ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Animal) da Universidade Federal do Espírito Santo como requisito parcial para a obtenção do grau de Doutor em Biologia Animal.

Vitória, ES
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"*A tarefa não é tanto ver aquilo que ninguém viu, mas pensar o que ninguém ainda pensou sobre aquilo que todo mundo vê.*"

Arthur Schopenhauer

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Resumo

Os gêneros de Bethylinae são claramente diferentes um do outro. A maioria das espécies Bethylinae é conhecida apenas pelo sexo feminino. Seus limites taxonômicos podem ser considerados bem estabelecidos, exceto para *Goniozus* Förster. Sem dúvida é o gênero com o mais alto grau de confusão taxonômica em relação a seus limites. Os caracteres importantes que delimitam *Goniozus* são compartilhados por vários gêneros de Bethylinae tornando a classificação incerta e dificultando a compreensão da evolução do caráter e da variação entre táxons. Atualmente, esta subfamília compreende aproximadamente 540 espécies descritas classificadas no mundo inteiro em oito gêneros existentes com baixo dimorfismo sexual. A filogenia das linhagens Bethylinae tem recebido atenção por Sorg em 1988, Polaszek & Krombein em 1994, Terayama em 1995 e De Ploëg & Nel em 2004. Em todas as análises realizadas há uma politomia basal entre *Eupsenella*, *Lytopsenella* e os demais gêneros de Bethylinae. Aqui objetivamos 1) revisar as espécies fósseis de Bethylinae, fornecendo descrições e ilustrações quando necessário. Além disso, fornecer uma chave nova para as espécies fósseis de Bethylinae; 2) reconhecer, definir e descrever *Afrobethylus* como um gênero novo para Bethylinae, além de suas espécie novas. Além disso, definir suas características diagnósticas, bem como fornecer uma chave para as espécies da região Afrotropical com base em fêmeas; 3) propor uma hipótese filogenética baseada em dados morfológicos dos gêneros de Bethylinae chamando atenção especial para as relações de *Eupsenella* e *Lytopsenella* com os outros gêneros desta subfamília; 4) investigar e discutir os principais caracteres diagnósticos dos gêneros Bethylinae. O material examinado foi fornecido por várias instituições. As descrições, lista de caracteres, matrizes de caracteres para análise cladística e chave, quando necessário, foram elaboradas com o software DELTA. As buscas para as árvores mais parcimoniosas foram realizadas com o software TNT. Aqui, com base nos nossos resultados, consideramos que o gênero fóssil *Protobethylus* De Ploëg & Nel, 2004 é um sinônimo júnior de *Eupsenella* Westwood, 1874. Além disso, com base em nosso resgate e compilação de toda a informação existente em Bethylinae a família fóssil Fushunochrysidae proposta por Hong em 2002 foi sinonimizada com Bethylidae Haliday, 1839. O único gênero desta família é *Fushunochrysites* Hong, 2002 e sua única espécie *F. eocenicus* Hong, 2002 foi estabelecida como sua espécie tipo. Aqui, propomos que a melhor alocação deste gênero monotípico em Bethylidae é em Bethylinae. *Fushunochrysites* exibe em sua asa anterior vários caracteres que também estão presentes em todos os membros de *Eupsenella*. Além disso, *Sinibethylus* Hong, 2002 da mina de carvão chinesa Xilutian é aqui

também sinonimizada com *Eupsenella*. Finalmente, a última sinonímia do gênero proposta aqui está relacionada à *Messoria* que foi descrita originalmente por Meunier em 1916. Aqui propomos *Messoria* como sinônimo júnior de *Goniozus* e transferir sua única espécie *Messoria copalina* Meunier, 1916 para *Goniozus*. Além disso, com base em uma incomum combinação de caracteres descrevemos *Afrobethylus* como um novo gênero Bethylinae. Este gênero de Bethylinae é o único exclusivamente Afrotropical. No contexto filogenético, as matrizes resultantes contêm um total de 61 espécies terminais de Bethylinae como grupo interno, com um total de 43 caracteres codificados para machos e um total de 87 espécies, 44 caracteres codificados para fêmeas. As análises de reamostragem baseadas em machos e fêmeas retornaram suporte para uma relação de grupo irmão entre todos os gêneros de Bethylinae existentes. Todos os gêneros foram recuperados como linhagens em ambas as análises, exceto *Goniozus* que foi recuperado como parafilético em todas as análises realizadas. Nosso mais notável resultado obtido foi à resolução da politomia basal existente em Bethylinae entre *Lytopsenella* e *Eupsenella* com os outros gêneros Bethylinae existentes. Em todas as análises realizadas, esses gêneros foram recuperados pela primeira vez como um grupo irmão entre si e separados dos demais gêneros em todas as análises realizadas. Com base em nossos resultados, discutimos os principais caracteres diagnósticos dos gêneros Bethylinae, presentes principalmente na antena, na asa anterior e, finalmente, pela primeira vez nas genitálias dos machos e das fêmeas. Em especial, sobre as asas anteriores em Bethylinae, sugerimos abordagens viáveis para à morfologia funcional da venação nos clados de Bethylinae. O presente estudo é o tratamento cladístico mais abrangente dedicado à compreensão da evolução dos gêneros de Bethylinae e o primeiro a considerar uma amostragem global das espécies desta subfamília. Concluímos que os caracteres morfológicos inexplorados, principalmente, das genitálias dos machos e das fêmeas podem oferecer dados adicionais relevantes para estimar de forma mais robusta a história filogenética deste grupo. Aqui, promovemos um primeiro passo para direcionar e encorajar futuras pesquisas em Bethylinae usando o arranjo de veias, linhas de flexão e caracteres da genitália dos machos e das fêmeas para a reconstrução filogenética.

Abstract

The genera of Bethylinae are clearly different one from another. The most of Bethylinae species are known only by the female sex. Their taxonomic boundaries can be considered well established, except for *Goniozus* Förster. Undoubtedly it is the genus with the highest degree of taxonomic confusion regarding its boundaries. The important characters delimiting *Goniozus* are also shared by several Bethylinae genera, making classification uncertain and hampering understanding of character evolution and variation between taxa. This subfamily currently comprises approximately 540 species described worldwide classified in eight extant genera with low sexual dimorphism. The phylogeny of Bethylinae lineages has received attention by Sorg in 1988, Polaszek & Krombein in 1994, Terayama in 1995 and De Ploëg & Nel in 2004. In all previous analyses performed there is a basal polytomy among *Eupsenella*, *Lytopsenella* and the remaining Bethylinae genera. Here we aimed 1) to review the fossil species of Bethylinae, providing descriptions and illustrations when necessary. In addition, o provide a new key to the fossil species of Bethylinae; 2) to recognize, define and describe *Afrobethylus* as a new Bethylinae genus, its new species. In addition, to define their diagnostic characteristics, as well as provide a key to species of Afrotropical region based on females; 3) to propose a phylogenetic hypothesis based on morphological data of the genera of Bethylinae drawing especial attention to *Eupsenella* and *Lytopsenella* relationships with the other genera of this subfamily; 4) to investigate and discuss the main diagnostic characters of Bethylinae genera. Examined material was provided by several institutions. The descriptions, character list, character matrices for cladistic analysis and key, when necessary, were elaborated with o software DELTA. The searches for the most parsimonious trees were carried out under the software TNT. Here, based on our results, we considered that the fossil genus *Protobethylus* De Ploëg & Nel, 2004 is a junior synonymous of *Eupsenella* Westwood, 1874. In addition, based on our rescue and compilation of whole the existing information in Bethylinae the fossil family Fushunochrysidae proposed by Hong in 2002 was synonymized with Bethylidae Haliday, 1839. The single genus of this family is *Fushunochrysites* Hong, 2002 and its single species *F. eocenicus* Hong, 2002 was established as its type-species. Here, we propose that the best placement of this monotypic genus in Bethylidae is into Bethylinae. *Fushunochrysites* displays on its forewing several characters that are also present in all members of *Eupsenella*. Moreover, *Sinibethylus* Hong, 2002 from Chinese Xilutian coal mine is here also synonymized with *Eupsenella*. Finally, the last synonymy of genus proposed here is related to *Messoria* that was described originally by Meunier in 1916. We here propose

Messoria as a new junior synonym of *Goniozus* and transfer its single *Messoria copalina* Meunier, 1916 to *Goniozus*. In addition, based on an unusual combination of characters never seen before to Bethylinae we describe *Afrobethylus* as a new Bethylinae genus. This Bethylinae genus is the unique excluviley Afrotropical. In the phylogenetic context, the resulting matrices contain a total of 61 species of Bethylinae terminals as ingroup, with a total of 43 characters were coded for males and a total of 87 species, 44 characters were coded for females. The resampling analyses based on both males and females returned support for a sister-group relationship among all extant Bethylinae genera. All genera were retrieved as lineages in both analyses, except *Goniozus* that was retrieved as paraphyletic in all analyses performed. Our most remarkable result obtained was the resolution of the existing basal polytomy in Bethylinae between *Lytopsenella* and *Eupsenella* with the other extant Bethylinae genera. In all analyses performed, these genera were retrieved by the first time as sister-group each other and separated from the other genera in all analyses performed. Based on our results, we discuss the main diagnostic characters of Bethylinae genera mainly present in the antenna, forewing, and finally by the first time in the male and female genitalia. In special, about the forewings in Bethylinae, we suggest practicable approaches to functional morphology to the venation in the Bethylinae clades. The present study is the most comprehensive cladistic treatment dedicated to the understanding of the evolution of the Bethylinae genera, and the first to consider a global sampling of species of this subfamily. We conclude that the morphological characters unexplored, mainly, of male and female genitalia might offer additional data relevant to more robustly estimate the phylogenetic history of this group. Here, we also promote a first step to direct and encourage future research in Bethylinae using the arrangement of forewing veins, flexion lines and male and female genitalia characters to phylogenetic reconstruction.

Apresentação

Rever nossa trajetória é sempre uma oportunidade interessante. Neste momento paramos para refletir sobre o caminho que trilhamos na direção tanto da nossa realização profissional quanto da nossa contribuição, nesse campo, ao desenvolvimento das instituições e da sociedade das quais fazemos parte.

Do ensino fundamental à entrada na Universidade Federal do Espírito Santo - UFES

Chamo-me Magno Suprani Ramos, nascido no dia 19/05/1982, filho único, de Maria da Penha Suprani Ramos e Domingos Machado Ramos, e tive minha infância, mais precisamente até meus seis anos de idade, vividos na Grande Vitória em diversos bairros quando por questões de trabalho meus pais se mudaram para o interior do Espírito Santo, distrito de Jacupemba em Aracruz.

Em Jacupemba iniciei meus estudos frequentando a escola Maria Inês Della Valentina. Antes de o ano letivo iniciar efetivamente minha mãe já cuidava da minha alfabetização, e esta atitude culminaria já nos primeiros meses de aula em um convite da diretora para remanejado e cursar a terceira série do ensino fundamental. Desde criança já demonstrava facilidade com as palavras e um grau alto de curiosidade para a idade. No entanto, mesmo apresentando todas as habilidades pedagógicas necessárias para cursar a terceira série meus pais preferiram me manter na primeira série por eu ainda ser muito pequeno em relação aos demais alunos. Nesta instituição estudei até completar a terceira série do ensino fundamental quando então retorno a Grande Vitória, especificamente ao bairro Ilha das Flores, em Vila Velha.

Ao chegar neste bairro novo, sou imediatamente matriculado na escola pública municipal de Ensino Fundamental Antônia Malbar, onde cursaria a quarta série do ensino fundamental. Ao término do ano letivo mais uma vez aprovado fui transferido para a escola pública municipal de Ensino Fundamental Macionilia Mauricio Bueno no bairro Paul, pois a escola pública municipal de Ensino Fundamental Antônia Malbar no bairro Ilha das Flores é somente para os alunos de primeira a quarta série.

Foi na escola “Macionilia Mauricio Bueno” agora com aulas frequentes no laboratório de ciências que minha curiosidade pelos seres vivos aumentou. Passei por conta de um trabalho escolar, em grupo, mas que preferi desenvolver sozinho a buscar mais informações nos livros de ciências e a “coletar” besouros mortos para exemplificação do conteúdo que

seria abordado no trabalho. Na verdade "coletava" tudo que se parecia com besouros, ao final do processo avaliativo descobri com ajuda dos professores de ciências que tinha "coletado" uma grande quantidade de insetos de ordens diferentes. Nesta escola cursei até a oitava série, completando então o ensino fundamental.

Após a conclusão do ensino fundamental, devido ao meu desempenho acima da média em todas as matérias cursadas até aquele momento prestei processo seletivo para receber bolsas de estudo no colégio Nacional. Até então esta era uma das principais referências no ensino, e consegui bolsa de 100% para cursar o primeiro ano do ensino médio. Tudo era muito diferente de tudo que eu estava acostumado em termos de rotina e estrutura de ensino com diversas atividades interdisciplinares, inclusive aos sábados. Para alunos bolsistas, como era meu caso, a média era de sete pontos, um ponto acima da média para os demais alunos. Diante dessa condição, fui "forçado" a me dedicar ainda mais aos estudos e as atividades para não ter minha bolsa de estudos cancelada. Ao término daquele ano letivo, consegui cumprir além do mínimo em termos de notas e fui aprovado. No entanto, fui informado que por questões administrativas e financeiras todas as bolsas integrais concedidas seriam suspensas para os próximos anos. Diante disso, a partir daquele momento o valor máximo de desconto seria de 50%, fora o material didático. Por questões financeiras, que não detalharei, ficou decido que não haveria a mínima chance de continuar naquela instituição nos anos seguintes.

Diante deste cenário, em busca de uma vaga para cursar as séries restantes do ensino médio meus pais tiveram muitas dificuldades para encontrar uma escola de ensino regular com segundo ano do ensino médio. Na época surgiu uma única opção, estudar no ensino técnico. Com base nisso, fui matriculado no Centro Estadual de Educação Técnica Vasco Coutinho. No "Vasco Coutinho" cursei segundo e terceiro ano na modalidade técnico em Administração. Nesse momento em especial, me afastei por dois anos de matérias como Geografia, História, Química, Física. A única disciplina que mesmo não constando na grade curricular do curso de Administração estava sempre presente em minhas leituras era Biologia. Nos tempos livres lia sobre conteúdos diversos e principalmente zoologia, em especial sobre os insetos. Confesso que nesses dois anos estudando no colégio "Vasco Coutinho" aprendi muito mais Biologia do que qualquer outro conteúdo relacionado ao ensino técnico de Administração.

Ao completar o ensino técnico no ano 2000, precisei de três tentativas para obter minha aprovação no vestibular da UFES para o curso de Ciências Biológicas. Até obter esta aprovação trabalhei no extinto "Consórcio Econômico" como consultor e também em uma

empresa chamada "*Bankinform*" voltada para a avaliação da situação de crédito dos potenciais clientes dos estabelecimentos. Durante esses meses de trabalho nestas empresas consegui algum dinheiro para arcar com o material, passe escolar, reprografia, alimentação e etc.

No ano de 2004 me matriculei para o primeiro semestre (2004/1) do curso de Ciências Biológicas Ciências Biológicas na UFES.

Trajetória acadêmica

Em Maio de 2004 ingressei no curso de Ciências Biológicas da Universidade Federal do Espírito Santo – UFES.

Já no primeiro período de graduação sondava uma área em que pudesse me inserir, mas já havia percebido que não era tão simples como eu imaginava. Somente depois de seis meses de curso, foi que efetivamente busquei algum professor da instituição que pudesse me orientar.

Em 2005, iniciei atividades de coleta de Quirópteros, juntamente com alunos ligados ao Laboratório de Estudos em Quirópteros, orientados pelo professor Dr. Albert David Ditchfield. Foram vários campos de coleta diferentes, tais como para o Parque Estadual Paulo César Vinha, antigo Parque Estadual de Setiba, Reserva Biológica de Duas Bocas e Estação Biológica Santa Lúcia. Nestes campos aprendi as principais técnicas de coleta de Quirópteros, montagem das redes de captura e identificação dos principais gêneros.

Por outro lado, concomitantemente, busquei informações sobre os laboratórios que teriam como objeto de estudo, insetos. De posse destas informações, chego ao hoje intitulado Instituto Bethylidae de Sistemática, coordenado pelo professor Dr. Celso Oliveira Azevedo para solicitar uma oportunidade de estágio. Neste momento, até mesmo por imaturidade estava trabalhando tanto com quirópteros quanto com insetos. Diante desse panorama, o professor Dr. Ceslo, teve uma conversa franca comigo sobre a importância de decidir o quanto antes na área a seguir. Depois de pensar a respeito, fiz a escolha pelo estudo dos insetos, algo que na verdade sempre me fascinou dentro da biologia. Inicialmente no Instituto Bethylidae de Sistemática, meu treinamento foi direcionado para a montagem de insetos em geral. Posteriormente, também recebi treinamento em montagem, organização e identificação de material biológico da família Bethylidae, objeto de estudo central do referido instituto, especificamente com o uso de chaves de identificação.

Após esse período inicial de treinamento, ainda no ano de 2005 recebi meu primeiro projeto de pesquisa "Organização dos Bethylidae (Hymenoptera) neotropicais da Canadian National Colection of Insects", trabalho este voltado para organização e triagem do material em gêneros oriundos da Canadian National Colection of Insects para região Neotropical. Para desenvolver tal projeto iniciei um estágio voluntário com carga horária mínima de 20h por semana. Este projeto foi desenvolvido durante um ano, culminando com a apresentação dos resultados obtidos na jornada de iniciação científica daquele mesmo ano. Em fevereiro de 2006 tive a minha primeira oportunidade de participar e apresentar resultados do meu estudo no XXVI Congresso Brasileiro de Zoologia, 2006, realizado na cidade de Londrina/PR.

No ano de 2006 fui já como estagiário bolsista CNPq/PIBIC, com enquadramento funcional de estagiário bolsista de iniciação científica responsável pelo trabalho intitulado "Sistemática dos grupos de espécie de *Apenesia* (Hymenoptera, Bethylidae), da região neotropical". Tal projeto tinha por finalidade realizar a taxonomia do gênero *Apenesia*, estudar o material e realizar a separação deste material biológico nos respectivos grupos de espécie.

No ano de 2007, os resultados parciais do projeto supracitado foram apresentados na jornada de iniciação científica daquele ano. Este projeto desenvolvido representa muito em minha carreira científica, pois foi a partir destes resultados obtidos que entre os anos de 2007-2008 me tornei responsável pela execução do projeto "Sinopse das espécies neotropicais do grupo brasiliensis (Hymenoptera, Bethylidae, *Apenesia*)", que culminaria futuramente na minha primeira publicação científica.

No ano de 2008 tive a oportunidade de participar e apresentar os resultados no XXVII Congresso Brasileiro de Zoologia, realizado em Curitiba/PR e também na jornada de iniciação científica daquele mesmo ano.

Este trabalho resultou em minha monografia no ano de 2009 e culminou e como citado acima na minha primeira publicação de um artigo científico, Ramos & Azevedo (2009), intitulado "Sinopse das espécies neotropicais do grupo brasiliensis do gênero *Apenesia* (Hymenoptera, Bethylidae)". Neste trabalho, foi realizada a taxonomia do grupo de espécies brasiliensis com elaboração de uma chave nova de identificação para machos da região Neotropical. Além disso, seis espécies novas foram descritas para a região, minhas primeiras espécies novas publicadas, e oito espécies já descritas tiveram sua distribuição geográfica ampliada neste estudo. Tal artigo foi publicado na revista "Iheringia Série Zoologia" (Volume impresso, v.99, p.349 - 349, 2009). No ano seguinte publiquei outro artigo com o gênero

Apenesia agora com o grupo de espécies *nitita*, Ramos et al. (2010), intitulado "Sinopse das espécies neotropicais do grupo *nitida* do gênero *Apenesia* (Hymenoptera, Bethylidae)" publicado também na revista "Iheringia Série Zoologia" (Impresso, v.100, p.309 - 309, 2010). Com o desenvolvimento destes artigos pude iniciar meu amadurecimento no processo de publicação, comportamento científico, além estimular meu espírito crítico e instrumentalizar a minha criatividade em função de uma proposta de pesquisa a qual busco desenvolver.

Paralelamente as minhas atividades de pesquisa realizei também estágio voluntário por dois anos na disciplina Zoologia dos Invertebrados III ministrada pelo Prof. Dr. Celso Oliveira Azevedo.

Após o término da minha graduação, prestei o processo seletivo de mestrado daquele ano, mas não fui aprovado por alguns décimos da prova de proficiência em língua inglesa de caráter eliminatório. No entanto, no mês de maio de 2009 me foi concedida a oportunidade de trabalhar com diretamente com a Coleção Entomológica da Universidade Federal do Espírito Santo – UFES.

No ano de 2009 tornei-me bolsista de Apoio técnico da coleção entomológica da UFES com carga horária de 40h por semana e regime de dedicação exclusiva. Foram desenvolvidas atividades de apoio técnico nível "A" sob a orientação do interveniente Marcelo Teixeira Tavares, no projeto "GESTÃO DA INFORMAÇÃO SOBRE A BIODIVERSIDADE NO ESTADO DO ESPÍRITO SANTO" objeto do convênio MCT/FAPES nº 01.0178.00/2005, tendo prazo de duração desta bolsa cinco meses (de 01/05-30/09/09). Naquele ano novamente me inscrevi para prestar o processo seletivo do mestrado da UFES. Diferentemente do ano anterior, após realizar seis meses de curso preparatório em inglês instrumental no centro de líguas da UFES atingi muito mais do que a pontuação mínima para a prova de proficiência em língua inglesa e também na prova de conhecimentos específicos em biologia animal, resultando na minha aprovação.

No mês de março de 2010 inicio minhas atividades de pesquisa no Programa de Pós-Graduação em Ciências Biológicas – PPGBAN em nível de mestrado. Para desenvolver o trabalho intitulado Revisão de *Eupsenella* Westwood (Hymenoptera, Bethylidae) recebi dois anos de bolsa de estudos da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CNPq). Com este projeto de mestrado desenvolvi minha dissertação de mestrado e a defendi no ano de 2012, alcançando então o título de mestre em Ciências Biológicas. Como resultado da minha pesquisa em nível de mestrado publico, agora em uma revista internacional, meu terceiro artigo científico, Ramos & Azevedo (2012), intitulado Revision of *Eupsenella*

Westwood, 1874 (Hymenoptera, Bethylidae) publicado na revista "Zootaxa" (v.3539, p.1, 2012).

Após concluir o mestrado, novamente realizo atividades de apoio técnico na coleção entomológica da UFES com carga horária de 40h por semana e regime de dedicação exclusiva. Realizei como bolsista de Apoio Técnico AT-B do projeto "N.E.S.H. – Núcleo de Excelência em Sistemática de Hymenoptera: ampliando fronteiras agrícolas e ambientais do Espírito Santo", processo número 52263010/2011, atividades técnicas de 01 de março de 2012 até 01 de março de 2013, sob a orientação do Prof. Dr. Celso Oliveira Azevedo.

Ao final do ano de 2012 me inscrevi no Programa de Pós-graduação em Ciências Biológicas – PPGBAN para prestar o processo seletivo em nível de doutorado. Obtive minha aprovação e no dia 01 de março de 2013 iniciaria as minhas atividades de pesquisa em nível de doutorado. Vale ressaltar que concomitantemente ao processo seletivo no PPGBAN também prestei concurso para ser professor da rede estadual de ensino do Espírito Santo, sendo também aprovado naquele mesmo ano, mas sem perspectivas até então de quando seria a chamada para assumir o cargo.

O projeto de doutorado teve como foco central a sistemática da subfamília Bethylinae. Como primeira ação do doutorado nos primeiros meses do ano de 2013 desenvolvi em parceria com renomados pesquisadores estudiosos de fósseis o trabalho, Ramos et al. (2014), intitulado "Revision of Bethylinae fossils (Hymenoptera: Bethylidae) from Baltic, Rovno and Oise amber, with comments on the Tertiary fauna of the subfamily" publicado na revista especializada da área Neues Jahrbuch fur Geologie und Palaontologie. Abhandlungen. (v.271, p.203 - 228, 2014). Tal trabalho foi publicado nos primeiros meses de 2014. O objetivo central desta pesquisa foi revisar as espécies fósseis da subfamília Bethylinae, descrever espécies fósseis novas e principalmente investigar se o gênero *Protobethylus*, De Ploëg & Nel (2004) poderia ou não ser considerado um gênero válido para Bethylinae. Este gênero fóssil foi minuciosamente investigado e com base nestas observações constatou-se que o mesmo apresentava muito mais semelhanças com *Eupsenella* Westwood, 1874 do que diferenças. Portanto, neste artigo argumentamos que seria mais prudente considera-lo como sinônimo júnior de *Eupsenella* Westwood. Toda essa investigação foi necessária como primeira ação do meu doutorado, pois *Protobethylus*, De Ploëg & Nel foi recuperado na filogenia proposta por De Ploëg & Nel no ano de 2004 em uma politomia basal com *Eupsenella* e *Lytopsenella*, Kieffer 1904.

Ainda no ano de 2013 participei do meu primeiro Workshop internacional organizado e coordenado pelo professor Dr. Celso Oliveira Azevedo intitulado ”N.E.S.H. – Núcleo de Excelência em Sistemática de Hymenoptera: ampliando fronteiras agrícolas e ambientais do Espírito Santo” sediado na Universidade Federal do Espírito Santo. No mês de julho deste mesmo ano, mais precisamente no dia 30 de julho, assumo meu cargo de servidor público efetivo do Governo do Estado do Espírito Santo na função de Professor efetivo do Ensino Médio na Escola Estadual de Ensino Fundamental e Médio Adolfina Zamprogno, no bairro Vila Garrido com carga horária de 25h semanais no turno matutino. A partir deste momento, minha jornada no doutorado estava restrita ao turno vespertino e parte do noturno.

Devido a esta jornada agora como professor pela manhã limitar meu tempo e possíveis visitas as coleções de interesse onde estariam depositados Bethylinae de interesse elaborei juntamente com meu orientador um plano de ação para que fosse possível viajar e visitar uma coleção entomológica importante no ano de 2015 durante as minhas férias escolares.

No ano de 2015, depois de cumpridas todas as metas estabelecidas no plano de ação, mais especificamente nos meses de janeiro e fevereiro visito e trabalho na coleção entomológica do Smithsonian Institution National Museum of Natural History – USNM (Washington, DC – EUA) na condição de pesquisador convidado com carga horária de 50h por semana e em regime de dedicação exclusiva. Nesta coleção realizei a análise e revisão de tipos de espécies pertencentes à subfamília Bethylinae (Hymenoptera; Bethylidae) com objetivo de finalizar o projeto de doutorado. Além disso, organizar e identificar de exemplares de Bethylidae pertencentes à coleção entomológica. Sem dúvida foi a melhor experiência de toda a minha jornada na Universidade Federal do Espírito Santo, tanto em nível profissional quanto pessoal. Fui recebido por Brian Harris (curador chefe) e Sean Brady (curador responsável pela coleção de Hymenoptera) que me proporcionaram acesso irrestrito a toda a coleção de Bethylidae, em especial a de Bethylinae. Além disso, forneceram toda a estrutura necessária para que eu estivesse munido das ferramentas necessárias para executar as pesquisas e análises de maneira produtiva. Como forma de retribuição, constatei juntamente com Brian Harris, um problema na documentação do museu para envio de material biológico para o Brasil. Por já ter trabalhado na coleção entomológica da UFES, e pela prática desenvolvida nos trâmites destes envios pude ajuda-lo decisivamente na obtenção dos documentos necessários para envio de material biológico agora sem nenhum tipo de problema com as autoridades aeroportuárias brasileiras.

No ano de 2016, analisando material biológico da fauna africana descobrimos espécimes bem peculiares com características diagnósticas de dois gêneros válidos para Bethylinae. Por meio de uma investigação taxonômica aprofundada foi possível reconhecermos que tais espécimes poderiam compor um gênero novo para a subfamília, condição confirmada alguns meses depois. Um artigo desenvolvido por Ramos & Azevedo (2016) relatando tal descoberta foi publicado na revista Zootaxa (Auckland. Print, v.4097, p.495 - 495, 2016) e foi intitulado "*Afrobethylus* Ramos & Azevedo, gen. nov., a new remarkable Afrotropical genus of Bethylinae (Hymenoptera: Bethylidae". Este correspondia a meu quinto artigo científico publicado, sendo meu primeiro gênero novo descrito não somente para a subfamília, mas para Bethylidae. Os resultados dessa pesquisa foram apresentados no XXXI Congresso Brasileiro de Zoologia, realizado em Cuiabá/MT, no de 2016. Ainda neste ano, juntamente com os professores Jonatha Liprandi Jaques, Fabiano Gambine Diir e da diretora da unidade de escola "Adolfina Zamprogno" Ângela Maria Soares submeti meu primeiro artigo científico na área da educação intitulado "Uso de espaços não formais de ensino institucionalizados: uma proposta de educação ambiental como prática interdisciplinar no Parque Estadual Paulo César Vinha/ES". Essa proposta tem como finalidade a utilização de espaços não formais na construção de conhecimento. Além disso, despertar o interesse de maneira criativa entre os alunos e oferecendo condições para os mesmos criarem uma consciência e sensibilização ecológica no cenário de desenvolvimento sustentável.

Uma das experiências relevantes da minha jornada acadêmica surgiu nos últimos meses do meu doutorado. Em virtude de um trabalho paralelo a minha tese de doutorado participei e desenvolvi em parceria com meu orientador e outros alunos de doutorado e pós-doutorado a análise filogenética das subfamílias de Bethylidae. Uma das decisões mais acertadas da minha caminhada foi ter feito a inscrição, mediante aconselhamento e incentivo do companheiro e amigo de doutorado Diego Barbosa, para participar do evento "35th Annual Meeting of the Willi Hennig Society", realizado em Buenos Aires no ano de 2016. Neste evento apresentamos os resultados parciais da análise filogenética das subfamílias de Bethylidae, somente com os dados morfológicos em forma de Poster/Painel do trabalho intitulado "Rescuing evolutionary history of Bethylidae subfamilies (Hymenoptera, Chrysidoidea) with implications on hosts of the parasitoid habit". Neste encontro dos membros da sociedade foi possível encontrar os principais autores, verdadeiros "ícones" da área filogenética e entender na íntegra o quão fascinante é esta área.

É com um sentimento de satisfação que chego ao final dessa breve apresentação. Penso que consegui transmitir, mesmo que em alguns momentos de forma mais simples e direta, o que considero ser o mais relevante na minha trajetória pessoal e profissional. Algumas escolhas conscientes dos caminhos que percorri e suas consequências, em alguns momentos, foram ousadas e arriscadas, mas das quais não me arrependo.

Finalmente, independente do parecer sinto-me grato por todas as oportunides a mim concedidas e também pelas dificuldades enfrentadas, pois estas também contribuíram como "combustível motivacional" para que eu pudesse chegar até esse momento.

Sobre os capítulos da tese

Esta tese apresenta quatro capítulos, todos eles relacionados aos Bethylinae. Os atos nomenclaturais aqui propostos são provisórios e inválidos para o ICZN. O primeiro capítulo apresenta a revisão taxonômica dos Bethylinae fósseis, com ênfase nos âmbares bálticos, Rovno e Oise. Devido ao perfil do trabalho este foi submetido ao periódico "Neues Jahrbuch für Geologie und Paläontologie" (https://www.schweizerbart.de/journals/njgpa). Neste trabalho foram descritas e ilustradas três espécies do âmbar Rovno e cinco do âmbar báltico, e foi confeccionada uma chave nova de identificação para as espécies fósseis de Bethylinae. Além destes resultados, o gênero fóssil *Protobethylus* De Ploëg & Nel, 2004 descrito por De Ploëg & Nel (2004) foi considerado como sinônimo júnior de *Eupsenella* Westwood, 1874. Estas proposições estão presentes no artigo intitulado "Revision of Bethylinae fossils (Hymenoptera: Bethylidae) from Baltic, Rovno and Oise amber, with comments on the Tertiary fauna of the subfamily" publicado por Ramos et al. (2014) (DOI: 10.1127/0077-7749/2014/0385). O texto do primeiro capítulo encontra-se de acordo com a formatação especificada do referido periódico. As figuras deste texto estão enumeradas já na formatação e sequência em que aparecem no artigo publicado.

O segundo capítulo apresenta a descrição alfa taxonômica do primeiro gênero de Bethylinae exclusivamente Afrotropical, *Afrobethylus* Ramos & Azevedo, 2016. Durante a triagem de amostras de material coletado no Madagascar (projeto "Terrestrial Arthropod Inventory of Madagascar") coordenado por Brian Fisher e alguns espécimes de Bethylinae da África do Sul (projeto "Afrotropical Hymenoptera Initiative") coordenado por Simon van Noort alguns espécimes chamaram nossa atenção. Tais espécimes apresentaram uma combinação de caracteres nunca antes vista para Bethylinae. Tais espécimes possuem antena com 10 flagelômeros, como em *Bethylus* Latreille, mas também asa anterior com célula segunda

radial fechada, como em *Sierola* Cameron. Neste trabalho, como principais objetivos, reconhecemos e descrevemos o gênero novo, *Afrobethylus* Ramos & Azevedo, 2016, e suas espécies novas. Além disso, foram definidas as características diagnósticas de *Afrobethylus* e uma chave de identificação baseada nas fêmeas do gênero foi confeccionada. Devido ao perfil do trabalho este foi submetido ao periódico "Zootaxa" (http://www.mapress.com/j/zt/). Estas proposições estão presentes no artigo intitulado "*Afrobethylus* Ramos & Azevedo, gen. nov., a new remarkable Afrotropical genus of Bethylinae (Hymenoptera: Bethylidae)" publicado por Ramos et al. (2016), (DOI: http://dx.doi.org/10.11646/zootaxa.4097.4.3). O texto do segundo capítulo encontra-se de acordo com a formatação especificada do referido periódico. As figuras deste texto estão enumeradas já na formatação e sequência em que aparecem no artigo publicado.

O terceiro capítulo apresenta hipótese filogenética dos gêneros de Bethylinae, com ênfase na busca pela solução das relações filogenéticas de *Eupsenella* e *Lytopsenella* com os demais gêneros de Bethylinae. Além disso, também pretende pela primeira vez trazer uma abordagem do ponto de vista de morfologia funcional para o arranjo das nervuras, linhas de flexão e áreas de deformação da asa anterior e investigar e discutir a evolução dos principais caracteres diagnósticos dos gêneros de Bethylinae. Pretendemos submetê-lo ao periódico "Insect Systematics & Evolution" (http://www.brill.com/insect-systematics-evolution) e, por isto, o texto já se encontra na formatação necessária do referido periódico.

O quarto capítulo pretende resgatar, reunir e compilar toda a informação existente em Bethylinae, considerando, inclusive, os resultados dos capítulos anteriores. Este último capítulo foi confeccionado dentro do escopo do projeto "Atlas dos gêneros de Bethylidae (Hymenoptera, Chrysidoidea)" e tem intenção de ser publicado como parte de um livro que objetiva organizar e atualizar o conhecimento a respeito dos gêneros de Bethylidae em escala global, através da construção de um manual ilustrado que pretende figurar entre as principais referências de Bethylidae. O livro ainda não tem data estabelecida para publicação, mas se dará posteriormente à publicação do capítulo 3 e, por isso, estará aberto a atualizações. A intenção é publicá-lo também no periódico "Zootaxa" (http://www.mapress.com/j/zt/) e, por isso, o texto já se encontra na formatação solicitada do referido periódico. Vale ainda ressaltar que pelo fato do quarto capítulo fazer parte de um livro não é apresentado aqui à parte de Material e Métodos e a literatura citada diz respeito à parte relacionada ao capítulo, pois estas sessões fazem parte de todo o livro e possuem juntas mais de 200 páginas. Além disto, as figuras deste texto estão enumeradas já na formatação e ordem de entrada do livro.

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CÁPITULO 1

REVISION OF BETHYLINAE FOSSILS (HYMENOPTERA: BETHYLIDAE) FROM BALTIC, ROVNO AND OISE AMBER, WITH COMMENTS ON THE TERTIARY FAUNA OF THE SUBFAMILY

Abstract

The known distribution and taxonomic variation of the previously described species *Lytopsenella kerneggeri* OHL are broadened. Eight new fossil species of Bethylinae are described and illustrated: *Eupsenella aulax* RAMOS & AZEVEDO sp. nov., *E. klesoviana* RAMOS & AZEVEDO sp. nov., *E. rossica* RAMOS & AZEVEDO sp. nov., *E. yantarnica* RAMOS & AZEVEDO sp. nov., *Goniozus definitus* RAMOS & AZEVEDO sp. nov., *Lytopsenella baltica* RAMOS & AZEVEDO sp. nov., *L. maritima* RAMOS & AZEVEDO sp. nov., and *Sierola rovniana* RAMOS & AZEVEDO sp. nov. *Protobethylus* DE PLOËG & NEL, 2004 is considered a junior synonym of *Eupsenella* WESTWOOD, 1874, and *Protobethylus eocenicus* DE PLOËG & NEL, 2004 is transferred from *Protobethylus* to *Eupsenella* as *E. eocenica* comb. nov. A key to the fossil species of Bethylinae is provided. This paper brings the total known fossil species of Bethylinae to 17.

Key words: Insecta, Chrysidoidea, Late Eocene, new combination, Rovno amber, Baltic amber.

1. Introduction

The analysis of fossils is important in understanding the events that shaped the evolutionary history of the planet. Previously, 49 fossil species have been reported for the family Bethylidae (Azevedo & Azar 2012). However, that report omitted *Cretobethylellus lucidus* RASNITSYN, 1990 from the Cretaceous of Transbaikalia (RASNITSYN 1990). Most of these species were described by BRUES (1923, 1933, 1939) based on Baltic amber from the Early Oligocene. The geographic distribution of bethylid fossils is limited to a few sites worldwide. Hitherto, nine species have been reported for the subfamily Bethylinae: *Goniozus contractus* (BRUES, 1933) (Oligocene, Baltic amber); *Goniozus respectus* SORG, 1988 (Miocene, Dominican amber); *Lytopsenella crastina* (BRUES, 1923) (Oligocene, Baltic amber); *Lytopsenella kerneggeri* OHL, 1995 (Late Eocene, Baltic amber); *Lytopsenella setigera* (BRUES, 1923) (Oligocene, Baltic amber); *Lytopsenella simplex* (BRUES, 1923) (Oligocene, Baltic amber); *Prosierola submersa* BRUES, 1933 (Early Oligocene, Baltic amber); *Protobethylus eocenicus* DE PLOËG & NEL, 2004 (earliest Eocene, Oise French amber); and *Sierola hastata* SORG, 1988 (Late Eocene, Baltic amber). Most of these species' types have been lost, except *L. kerneggeri* (deposited at the Geologisch Paläontologisches Institut und

Museum der Universität Hamburg) and *P. eocenicus* (deposited at the Muséum national d'Histoire naturelle, Paris).

Here, eight new species are added to the subfamily, and a new combination is proposed. *Protobethylus eocenicus* DE PLOËG & NEL, 2004, hitherto listed in *Protobethylus*, is transferred to *Eupsenella* as a new combination. Thus, the total known fossil species of Bethylinae are increased to 17.

The main aim of the present paper is to describe and illustrate three new species from the Upper Eocene Rovno amber and five new species from Baltic amber and to provide a new key to the fossil species of Bethylinae.

2. Material and methods

The specimens from Rovno amber were mined from the Klesov amber deposit (northern Rovno region; see PERKOVSKY et al. 2010) and obtained from the state 'Ukramber' factory (Rovno). The specimens from Baltic amber were extracted in Yantarny, Kaliningrad region, Russia, at a local mine in the Blue Ground of Prussia Formation. Finally, the specimen from Oise French amber was extracted from Le Quesnoy, Chevrière, Creil region, in level MP7 of the Dormaal mammal fauna.

Rovno amber is usually considered similar in age to the Baltic amber deposits (Late Eocene, ca. 36-37 million years (My); ALEKSANDROVA & ZAPOROZHETS 2008), whereas Oise amber is much older in age (53 My; see the detailed discussion by NEL et al. 1999).

Institutional abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris; PIN: A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow; SIZK: I.I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine in Kiev; UFES: Universidade Federal do Espírito Santo, Brazil.

Measurements and indices used in this study are as follows: body length was measured from the anterior most point of the clypeus to the posterior margin of the last metasomal segment, excluding male genitalia or female sting; LH, length of head, was measured in frontal view, from vertex crest to median anterior margin of clypeus; WH, maximum width of head, was measured in frontal view, including eyes; WF, narrowest width of frons, measured in frontal view, usually around level bottom of eyes; HE, height of eye, was measured in lateral view, across its maximum height (length); OOL, ocello-ocular line, was measured in latero-dorsal view, the shortest distance from eye top to posterior ocellus; WOT, width of ocellar triangle, was measured in frontal view, maximum width, including ocelli; DAO, diameter of anterior

ocellus, was measured in frontal view; distance of ocellar triangle to vertex: was measured in dorso-posterior view, distance from posterior ocellus to vertex crest; and VOL, vertex-ocular line, was measured in dorsal view, distance from eye top to vertex crest.

The nomenclature of integument sculpture follows HARRIS (1979), and general terms follow EVANS (1964), AZEVEDO (1999). The nomenclature of wing venation follows RAMOS & AZEVEDO (2012).

Symbols of wing venation: C: Costal cell; R: Radial cell; 1Cu: First cubital cell; 1R1: First radial 1 cell; 2R1: Second radial 1 cell; 1M: First medial cell (areolet); Rs*a*: First section of Rs vein; Rs*b*: Second section of Rs vein; Rs*c*: Third section of Rs vein; M: M vein; RS+M: RS+M vein; Cu*a*: First section of Cu vein (more details see RAMOS & AZEVEDO 2012, figs. 1-2).

3. Descriptions

The descriptions were performed with the software DELTA (Descriptive Language for Taxonomy) developed by DALLWITZ (1980), and DALLWITZ ET AL. (1999). Images were captured using the extended-focus system Leica Application Suite (LAS) – Version 4.1.0 [Build 1264] that feeds image data to a desktop computer. The captured stacks were exported, and combined in a single in-focus image using Helicon Focus v5.2.16, and later edited in Adobe Photoshop.

3.1. Key to fossil species of Bethylinae

1. Forewing with six closed cells (Figs 3, 7, 11, 16, 25, 35, 38, 44, 48, 49A, 50B) 2
- Forewing with five or less closed cells (Figs 31, 53) 12

2. Forewing with 1R1 cell longer than or as long as 2R1 cell (Figs 3, 7, 16, 18, 25); notauli always present (Figs 4, 6, 11, 17, 21, 24)……3
- Forewing with 1R1 shorter than 2R1cell (Figs. 35, 38, 44, 48); notauli usually absent (Figs 34, 36, 43, 44) ……...7

3. Propodeal disc with median longitudinal carina (Figs 6, 11, 21, 27) ……4
- Propodeal disc without median longitudinal carina (Figs. 1, 4).....*Eupsenella eocenica* (DE PLOËG & NEL) comb. nov.

4. Notauli uniformly narrow (Fig. 33); 1M cell of forewing subtriangulate (areolet) (Fig. 16)……...5

- Notauli strongly wide posterad (Fig. 27); 1M cell of forewing almost elliptical (areolet) (Fig. 27) ……*Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov.
5. RS+M vein of forewing shorter than Rs*a* (Figs. 7, 18)……6
- RS+M vein of forewing as long as Rs*a* (Fig. 16)……...*Eupsenella klesoviana* RAMOS & AZEVEDO sp. nov.

6. Pronotal disc with transversal furrow deep near posterior margin (Figs 5, 6, 9); vertex crest straight (Fig. 8) ……*Eupsenella aulax* RAMOS & AZEVEDO sp. nov.
- Pronotal disc without transversal furrow deep near posterior margin (Figs. 17, 21); vertex crest slightly concave medially (Fig. 19 ……*Eupsenella rossica* RAMOS & AZEVEDO sp. nov.

7. Notauli absent or when present ill-defined (Figs 34, 36, 43, 47) ……..8
- Notauli present and well-defined (see Brues 1933: 127, Fig. 68)…….*Lytopsenella simplex* (BRUES)

8. Vertex crest convex (Fig. 46); propodeal disc with median longitudinal carina incomplete (Fig. 47)……...9
- Vertex crest straight (Figs. 34, 37, 41); propodeal disc without median longitudinal carina (Figs 34, 42)…….10
9. Rs*a* slightly inclined toward tegula (Fig. 49A, B)……*Lytopsenella maritima* RAMOS & AZEVEDO sp. nov.
- Rs*a* subperpendicular to anterior margin of forewing (Fig. 48)……..*Lytopsenella baltica* RAMOS & AZEVEDO sp. nov.

10. Pronotal disc as long as mesoscutum (see BRUES 1933: 126, 128)……11
- Pronotal disc shorter than mesoscutum (Figs. 34, 36, 43)……...*Lytopsenella kerneggeri* OHL

11. Bristly hairs of vertex crest long (see BRUES 1933: 126)…*Lytopsenella setigera* (BRUES)
- Bristly hairs of vertex crest short (see BRUES 1933: 128)…….*Lytopsenella crastina* (BRUES)

12. 2R1 cell of forewing open (see Brues 1933: 128, 129)……13
- 2R1 cell of forewing closed (Fig. 53)……..……...16

13. Propodeal disc with pair of anterior pits (see BRUES 1933: 128,129); triangular area on propodeal disc absent (see Brues 1933: 128, 129……*Prosierola submersa* BRUES
- Propodeal disc without anterior pits (see Sorg 1988, figs. 22B, 136D, E; see BRUES 1933:

130; Fig. 29); triangular area on propodeal disc present (see Sorg 1988, figs. 22A, B; 136 D, E; see BRUES 1933: 130; Fig. 29)…….14

14. R*s*c ending abruptly toward anterior margin of forewing (see BRUES 1933: 130; Fig. 28); First medial cell (1M) of forewing almost elliptical (areolet) (see BRUES 1933: 130; Fig. 28)…….15
- R*s*c ending gently toward anterior margin of forewing (see SORG 1988, Fig. 22 A); 1M cell of forewing subtriangulate (areolet) (see Sorg 1988, Fig. 22 A)……*Goniozus respectus* SORG

15. Pronotal disc longer than mesoscutum (see Brues 1933: 130); malar space very short (see Brues 1933, pg. 130); anterior margin of forewing with conspicuous bristly hairs (see Brues 1933: 130) ……*Goniozus contractus* (BRUES)
- Pronotal disc shorter than mesoscutum (Fig. 32); malar space evident (Fig. 28); anterior margin of forewing without conspicuous bristly hairs (Fig. 31)……*Goniozus definitus* RAMOS & AZEVEDO sp. nov.

16. R, 1Cu, and 1M cells nebulous (Fig. 53)…*Sierola rovniana* RAMOS & AZEVEDO sp. nov.
- R, 1Cu, and 1M cells tubular (see Sorg 1988, fg. 20B)……...*Sierola hastata* SORG

3.2. Systematic palaeontology

Order Hymenoptera LINNAEUS, 1758

Family Bethylidae HALIDAY, 1839

Subfamily Bethylinae DALLA TORRE, 1898

Genus *Eupsenella* WESTWOOD, 1874

(Syn.: *Protobethylus* De Ploëg & Nel, 2004: 75, Type species: *Protobethylus eocenicus* DE PLOËG & NEL, 2004, by monotypy, syn. nov.)

Type species: *Eupsenella agilis* WESTWOOD, 1874, by monotypy.

Eupsenella eocenica (DE PLOËG & NEL, 2004) comb. nov.

Figs. 1-4

Material examined: Holotype specimen PA2436, (sex uncertain), in collection de Ploëg, housed in the Muséum National d'Histoire Naturelle, Paris (MNHN).

Occurrence: Lowermost Eocene, Le Quesnoy, Chevrière, region of Creil, Oise department, France.

Remarks: This species was originally described as *Protobethylus eocenicus* by DE PLOËG & NEL (2004). *Protobethylus* DE PLOËG & NEL, 2004 was established as a monotypic genus with *P. eocenicus* as its type species. The general habitus of this species closely resembles that of *Eupsenella* WESTWOOD, 1874. According to DE PLOËG & NEL (2004), the generic status of *Protobethylus* is based on its simple hind coxae and propodeal disc with the posterior transverse carina present but weak and the median longitudinal and discal carinae absent. However, the general habitus of *Protobethylus* is superfcially similar to that of *Eupsenella*. Based on photographs of the type species, *Protobethylus* exhibits several characters that are also present in all members of *Eupsenella*. The main characters found in both genera are the median clypeal lobe with the median carina continuing well up the frons, the notauli present and well-defined, the prosternum expanded and excavated medially, the forewing with six closed cells, the 2R1 cell ending abruptly toward the anterior margin of the forewing, the 1R1 cell as long as the 2R1 cell, and the complete ventral keel on the petiole.

Notably, DE PLOËG & NEL (2004) considered the character of simple, spineless hind coxae to represent a crucial difference between *Protobethylus* and *Eupsenella*. However, this character is also found in some extant *Eupsenella* species, such as *E. inggarda* RAMOS & AZEVEDO, 2012. This character is highly variable among *Eupsenella* species, ranging from almost imperceptible to clearly visible (see RAMOS & AZEVEDO 2012). Therefore, the character of simple, spineless hind coxae does not support the distinction between *Protobethylus* and *Eupsenella*. Considering this evidence, we are convinced that these genera are synonymous. We here propose *Protobethylus* DE PLOËG & NEL, 2004 as a new junior synonym of *Eupsenella* WESTWOOD, 1874 and transfer *Protobethylus eocenicus* DE PLOËG & NEL, 2004 to *Eupsenella*.

Eupsenella aulax RAMOS & AZEVEDO sp. nov.

Figs. 5-12

Etymology: The specific epithet *aulax*, from Latin, means ‘furrow’ in allusion to the transversal furrow deep near the posterior margin of pronotal disc.

Material examined: Holotype. Ukraine, Klesov, Rovno amber, 1 female, nº K-3986 (SIZK); Baltic amber, Baltic seacoast area, 1 female, 1307–1492 (UFES).

Occurrence: Rovno amber, Ukraine, Upper Eocene.

Diagnosis: Mandible with four sharpened apical teeth. Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Ocelli small. Vertex crest straight. Pronotal disc with transversal furrow deep near posterior margin, and longer than the mesoscutum. Notaulus present, and uniformly narrow. Forewing with 1M cell present, and closed; 1R1 cell as long as 2R1 cell; C cell widening distally.

Variation: Body lengths 2.5-3.3 mm; LFW 1.8-1.9 mm; clypeus with median carina strongly arched in profile; pronotal disc without transversal furrow; pronotal disc with posterior margin slightly sinuous; notaulus slightly wide posterad; propodeal disc with median longitudinal carina evident.

Description: Holotype, female, body length 3.3 mm, LFW 1.9 mm. Head. – Head subquadrate in dorsal view, as long as wide. Mandible with four sharpened apical teeth, two lowermost teeth as long as upper ones. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 11:6:5:5:5. Eye gibbous, large, > 0.5 x LH, glabrous. Ocelli small, ≤ 0.30 x WOT, 0.16 x WOT. HE 0.6 x LH. WH 1.0 x LH. WF 0.6 x WH. WF 1.0 x HE. OOL 1.33 x WOT. VOL 0.3 x HE. Vertex crest 6.0 x DAO. DAO 0.05 x WF. Distance between posterior ocelli 6.0 x DAO. Ocellar triangle not compact. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight.

Mesosoma. – Pronotal disc coriaceous, 0.5 x as long as wide, anterior corner rounded, anterior margin straight, posterior margin slightly concave medially; transversal furrow deep near posterior margin, longer than the mesoscutum. Mesoscutum 0.38 x as long as wide, coriaceous. Notaulus present, uniformly narrow, convergent posteriorly. Scutellum with scutellar fovea elliptical, narrowed. Mesopleuron coriaceous, mesopleural pit deep. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subpentagonal. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.19 x LFW. M vein straight. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* straight. Distal margin of Rs*c* convex, ending abruptly toward anterior margin of forewing. RS+M vein 1.0 x Rs*a*. M vein 1.5 x Rs*a*. Cu*a* vein 1.75 x Rs*a*. Rs*a*

subperpendicular to anterior margin of forewing. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved.
Metasoma. – 2.5 x longer than wide.
Male unknown.

Remarks: This species is similar to *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. in having large eyes, an expanded prosternum, and the distal margin of Rs*c* ending abruptly toward the anterior margin of the forewing. However, *Eupsenella aulax* RAMOS & AZEVEDO sp. nov. has small ocelli and a deep transverse furrow near the posterior margin of the pronotal disc, whereas *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. has large ocelli and lacks a deep transverse furrow near the posterior margin of the pronotal disc.

Eupsenella klesoviana RAMOS & AZEVEDO sp. nov.
Figs. 13-16

Etymology: The specific epithet *klesoviana* in allusion to the Klesov where the specimen was collected.

Material examined: Holotype. Ukraine, Klesov, Rovno amber, 1 female, nº K-5010 (SIZK).

Occurrence: Rovno amber, Ukraine, Upper Eocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Notaulus present, and uniformly narrow. Forewing with the 1R1 cell as long as 2R1 cell; 1M cell subtriangulate; the 1R1 cell of forewing shorter than 2R1 cell; C cell evenly narrow; RS+M vein as long as Rs*a*.

Description: Holotype, female, body length 2.9 mm, LFW 1.8 mm. Head. – Head subquadrate in dorsal view, as long as wide.
Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 9:6:5:5:5. Eye not gibbous, large, > 0.5 x LH, glabrous. HE 0.55 x LH. WH 1.0 x LH. WF 0.5 x WH. WF 1.0 x HE. VOL 0.33 x HE.

Mesosoma. – Pronotal disc coriaceous, 0.35 x as long as wide, anterior corner rounded. Mesoscutum 0.22 x as long as wide. Notaulus present, uniformly narrow, convergent posteriorly. Mesopleuron coriaceous, mesopleural pit shallow.

Wings. – Macropterous. Forewing with 1M cell present, closed, subtriangulate. 1R1 cell present, 1R1 cell 1.0 x 2R1 cell. C cell evenly narrow. 2R1 cell closed, 0.16 x LFW. M vein straight. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* slightly convex. Distal margin Rs*c* convex, ending abruptly toward anterior margin of forewing. RS+M vein 1.0 x Rs*a*. M vein 1.33 x Rs*a*. Cu*a* vein 1.66 x Rs*a*. Rs*a* slightly inclined toward tegula. Stigma not expanded, rectangular, distal stigmal margin truncate.

Legs. – Profemur 1.6 x longer than wide. Claws bifid, curved.

Metasoma. – 1.9 x longer than wide.

Male unnknown.

Remarks: This species is similar to *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. in having the notauli present and convergent posteriorly and the distal margin of Rs*c* convex, ending abruptly toward the anterior margin of the forewing. However, *Eupsenella klesoviana* RAMOS & AZEVEDO sp. nov. has the notaulus uniformly narrow, the 1M cell subtriangulate, and the 1R1 cell of the forewing shorter than the 2R1 cell, whereas *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. has the notaulus strongly widened posterad, the 1M cell elliptical, and the 1R1 cell of the forewing as long as the 2R1 cell.

Eupsenella rossica RAMOS & AZEVEDO sp. nov.

Figs. 17-22

Etymology: The specific epithet *rossica* is in allusion to the standard latinized adjective based on Russia where the specimen was collected.

Material examined: Holotype. Russia, Baltic amber, 1 female, PIN 964/130.

Occurrence: Baltic amber, Russia, Oligocene.

Diagnosis: Mandible with four sharpened apical teeth. Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Vertex crest

slightly concave medially. Pronotal disc with posterior margin slightly concave medially, and longer than the mesoscutum. Parapsidal furrows ill-defined. Notauli uniformly narrow. Forewing with the 1R1 cell as long as 2R1 cell; M vein straight. C cell evenly narrow.

Description: Holotype, female, body length 2.5 mm, LFW 1.6 mm. Head. – Head subrectangular in dorsal view, wider than long. Maxillar palpus with six palpomeres. Labial palpus with three palpomeres. Mandible with four sharpened apical teeth, two lowermost teeth as long as upper ones. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 10:6:3:3:3. Eye gibbous, large, > 0.5 x LH, glabrous. HE 0.59 x LH. WH 1.14 x LH. WF 0.52 x WH. WF 1.0 x HE. VOL 0.23 x HE. Vertex crest slightly concave medially.

Mesosoma. – Pronotal disc coriaceous, 0.48 x as long as wide, anterior corner rounded, anterior margin straight, posterior margin slightly concave medially, longer than the mesoscutum. Mesoscutum 0.47 x as long as wide, coriaceous. Notaulus present, uniformly narrow, convergent posteriorly. Parapsidal furrows present, ill-defined. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subtriangulate. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell evenly narrow. 2R1 cell closed, 0.12 x LFW. M vein straight. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* slightly convex. Distal margin of Rs*c* convex, ending abruptly toward anterior margin of forewing. Rs*a* slightly inclined toward tegula. Stigma expanded, rectangular, distal stigma margin truncate.

Legs. – Profemur 0.57 x longer than wide. Claws bifid, curved.

Metasoma. – 2.5 x longer than wide.

Male unknown.

Remarks: This species is similar to *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. in having the clypeus with an angulate median clypeal lobe and the median carina continuing well up the frons, the prosternum expanded and completely excavated medially, and the 1R1 cell as long as the 2R1 cell. However, *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. has the vertex crest slightly concave medially, the notaulus uniformly narrow, the pronotal disc longer than the mesoscutum, and the M vein traight, whereas *Eupsenella yantarnica* RAMOS

& AZEVEDO sp. nov. has the vertex crest straight, the notaulus strongly widened posterad, the pronotal disc as long as the mesoscutum, and the M vein convex.

Eupsenella yantarnica RAMOS & AZEVEDO sp. nov.

Figs. 23-27

Etymology: The specific epithet *yantarnica* is in allusion to the location Yantarny, where the specimen was collected.

Material examined: Holotype. Russia, Baltic amber, 1 female, PIN 964/120.

Occurrence: Baltic amber, Russia, amber.

Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Vertex crest straight. Pronotal disc as long as the mesoscutum. parapsidal furrows ill-defined, almost absent. Notaulus strongly wide posterad. Propodeal disc with median longitudinal carina present. Forewing with first medial cell closed, and almost elliptical; 1R1 cell as long as 2R1 cell; 1M cell almost elliptical; the M vein convex; C cell widening distally.

Description: Holotype, female, body length 2.7 mm, LFW 2.0 mm. Head. – Head subquadrate in dorsal view, as long as wide.

Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 7:3:3:3:3. Eye not gibbous, large, > 0.5 x LH, glabrous. Ocelli small, ≤ 0.30 x WOT, 0.30 x WOT. HE 0.54 x LH. WH 1.0 x LH. WF 0.5 x WH. WF 0.94 x HE. OOL 2.0 x WOT. VOL 0.38 x HE. Vertex crest 3.0 x DAO. DAO 0.13 x WF. Distance between posterior ocelli 1.5 x DAO. Ocellar triangle not compact. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight. Mesosoma. – Pronotal disc coriaceous, 0.5 x as long as wide, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially, as long as the mesoscutum. Mesoscutum 0.44 x as long as wide, coriaceous. Notaulus present, well defined; strongly wide posterad, convergent posteriorly. Parapsidal furrows illdefined. Scutellum with scutellar fovea eliptical, narrowed. Propodeal disc with median longitudinal carina present. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, almost elliptical. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell widening distally. 2R1 closed, 0.11 x LFW. M vein convex. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* straight. Distal margin of Rs*c* convex, ending abruptly toward anterior margin of forewing. RS+M vein 0.25 x Rs*a*. M vein 1.0 x Rs*a*. Cu*a* vein 1.5 x Rs*a*. Rs*a* slightly inclined toward tegula. Stigma expanded, rectangular, distal stigma margin truncate.
Legs. – Profemur 0.45 x as long as wide. Claws bifid, curved.
Male unknown.

Remarks: This species differs from the foregoing species in having the parapsidal furrows ill-defined and almost absent, the notaulus strongly widened posterad, the 1M cell almost elliptical, and the M vein convex.

Genus *Goniozus* FÖRSTER, 1856
(Syn.: *Parasierola* CAMERON, 1883: 197; type species: *Parasierola testaceicornis* CAMERON, 1883, by monotypy; *Progoniozus* KIEFFER, 1905: 105; type species: *Perisemus floridanus* ASHMEAD, 1887, by original designation; *Perisierola* KIEFFER, 1914: 533; type species: *Parasierola gallicola* KIEFFER, 1905, designated by MUESEBECK & WALKLEY (1951)).

Type species: *Bethylus claripennis* FÖRSTER, 1851, designated by ASHMEAD, 1893.

Goniozus definitus RAMOS & AZEVEDO sp. nov.
Figs. 28-32

Etymology: The specific epithet *definitus*, from Latin, means ‘defined, well-marked’ in allusion to triangular area well-defined of the propodeal disc.

Material examined: Holotype. Russia, Baltic amber, 1 female, PIN 363/138.

Occurrence: Baltic amber, Russia, Oligocene.

Diagnosis: Mandible with four sharpened apical teeth. Median clypeal lobe with median carina continues on well up the frons. Antennal scape not gibbous, and cylindrical. Malar space evident. Ocellar triangle compact. Vertex crest straight. Pronotal disc shorter than the mesoscutum. Notaulus absent. Propodeal disc with triangular area welldefined; median longitudinal carina absent; discal carina absent. Forewing with anterior margin of forewing without conspicuous bristly hairs; 1R1 cell absent; Rs*a* subperpendicular to anterior margin of forewing.

Description: Holotype, female, body length 3.1 mm, LFW 2.1 mm. Head. – Head subquadrate in dorsal view, as long as wide. Mandible with four sharpened apical teeth, two lowermost teeth larger than upper ones. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. Antennal scape not gibbous, cylindrical. Malar space evident. First five antennal segments in ratio of about 9:4:4:4:4. Eye not gibbous, glabrous. Ocelli large, > 0.30 x WOT, 0.4 x WOT. HE 0.5 x LH. WH 1.0 x LH. WF 0.7 x WH. WF 1.4 x HE. OOL 1.4 x WOT. VOL 0.5 x HE. Vertex crest 2.5 x DAO. DAO 0.14 x WF. Distance between posterior ocelli 2.5 x DAO. Ocellar triangle compact. Anterior ocellus not surpassing imaginary top eye line. Vertex crest straight.

Mesosoma. – Pronotal disc coriaceous, 0.6 x as long as wide, anterior corner rounded, posterior margin slightly concave medially, shorter than the mesoscutum. Mesoscutum 0.38 x as long as wide. Notaulus absent. Scutellum with scutellarfovea elliptical, narrowed. Propodeal disc with triangular area well-defined, median longitudinal carina absent, discal carina absent. Mesopleuron coriaceous, mesopleural pit shallow. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subpentagonal. Anterior margin of forewing without conspicuous bristly hairs. M vein straight. 1R1 cell of forewing absent. C cell evenly narrow. 2R1 cell open. Rs*a* perpendicular to anterior margin of forewing. Distal margin of Rs*a* ending abruptly toward anterior margin of forewing. RS+M vein 0.8 x Rs*a*. M vein 1.2 x Rs*a*. Cu*a* vein 1.6 x Rs*a*. Rs*a* slightly inclined toward tegula. Stigma expanded, rectangular, distal stigma margin truncate.

Legs. – Profemur 1.9 x longer than wide. Claws bifid, curved.

Metasoma. – 2.6 x longer than wide.

Male unknown.

Remarks: This species is similar to *Goniozus contractus* (BRUES, 1933) in having large eyes, the mesoscutum lacking notauli, the propodeal disc lacking a median longitudinal carina, the 2R1 cell open, and the 1M cell closed. However, *G. definitus* RAMOS & AZEVEDO sp. nov. has the antennal scape non-gibbous and cylindrical, the malar space evident, the pronotal disc shorter than the mesoscutum, and the anterior margin of the forewing without conspicuous bristly hairs, whereas *G. contractus* has the antennal scape gibbous and not strongly flattened, the malar space very short, the pronotal disc slightly longer than the mesoscutum, and the anterior margin of the forewing fringed with conspicuous, short, bristly hairs that extend from near the end of the basal cell to the apex of the stigma.

Genus *Lytopsenella* KIEFFER, 1911

Type species: *Eupsenella herbsti* KIEFFER, 1911, by original designation.

Lytopsenella kerneggeri OHL, 1995
Figs. 33-44

Material examined: Holotype. Female: Baltic amber (Upper Eocene), Hamburg (Nr. 24/85), University of Hamburg (Typ.-Kat. Nr. 3621). New material: Ukraine, Klesov, Rovno amber, 1 female, k-7923, 7915–30; 1 female, k-3553 (SIZK); Russia, Baltic amber, 1 female, PIN 964/129.

Occurrence: Rovno amber, Ukraine, and Baltic amber, Russia; Upper Eocene.

Variation: Body length 3.0–3.54 mm; LFW 1.9–2.5 mm; median longitudinal carina present, very short; mesoscutum clearly longer the mesoscutum; posterior margin of propodeal disc strongly concave; RS+M vein 0.75 x Rs*a*; M vein 1.5 x Rs*a*; Cu*a* vein 1.75 x Rs*a*; Rs*a* slightly inclined toward tegula; C cell clearly widening distally; vertex crest with several long, and wide setae; the 2R1 cell 1.35 x 1R1 cell.

Remarks: This species was previously known only from a single specimen from Baltic amber and is here recorded for the first time from Rovno amber.

Lytopsenella baltica RAMOS & AZEVEDO sp. nov.

Figs. 45-48

Etymology: The specific epithet *baltica* is in allusion to the coast of the Baltic Sea, where the specimen was collected.

Material examined: Holotype. Baltic amber, coast of Baltic Sea, 1 female, 0906 – 0991 (UFES).

Occurrence: Baltic amber, coast of Baltic Sea, Upper Eocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons, straight in profile. Vertex crest convex. Notaulus absent. Forewing with the distal margin of Rs*c* convex. 1M cell subquadrate.

Description: Holotype, Female, Body length 2.6 mm, LFW 2.2 mm.

Head. – Head subtriangular in dorsal view, longer than wide. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons, almost straight in profile. First five antennal segments in ratio of about 7:2:3:3:3. Eye gibbous, large, > 0.5 x LH, glabrous. Ocelli large, > 0.30 x WOT, 0.33 x WOT. HE 0.54 x LH. WH 0.88 x LH. WF 0.56 x WH. WF 0.9 x HE. OOL 1.66 x WOT. VOL 0.3 x HE. Vertex crest 3.0 x DAO. DAO 0.1 x WF. Distance between posterior ocelli 3.0 x DAO. Ocellar triangle not compact. Anterior ocellus not surpassing imaginary top eye line. Vertex crest convex.

Mesosoma. – Pronotal disc coriaceous, 0.4 x as long as wide, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially; as long as wide the mesoscutum. Mesoscutum 0.50 x as long as wide, coriaceous. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed.

Wings. – Macropterous. Tegula with setae. Forewing with 1M cell present, closed, subquadrate. 1R1cell of forewing present, 1R1 cell 0.86 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.22 x LFW. M vein straight. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* arched. Distal margin of Rs*c* convex, ending gently toward anterior margin of forewing. RS+M vein 0.8 x Rs*a*. M vein 1.0 x Rs*a*. Cu*a* vein 1.4 x Rs*a*. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved. Rs*a* subperpendicular to anterior margin of forewing.

Metasoma. – 2.6 x longer than wide.
Male unknown.

Remarks: This species is similar to *Lytopsenella kerneggeri* OHL in having large eyes, the vertex crest with a series of long bristly hairs, the notauli absent, and the costal cell (C) widening distally. However, *Lytopsenella baltica* RAMOS & AZEVEDO sp. nov. has a median clypeal lobe with the median carina nearly straight in profile, the vertex crest convex, the distal margin of the third section of the Rs vein (Rs*c*) convex, and the 1M cell subquadrate, whereas *L. kerneggeri* OHL has a median clypeal lobe with the median carina strongly arched in profile, the vertex crest straight, the distal margin of Rs*c* nearly straight, and the 1M cell subpentagonal.

Lytopsenella maritima RAMOS & AZEVEDO sp. nov.
Figs. 49A, B, 50C, D

Etymology: The specific epithet *maritima*, from Latin, means 'seacoast' in allusion to the coast of the Baltic Sea, where the specimens were collected.

Material examined: Holotype. Baltic amber, coast of Baltic Sea, 1 female and 1 male allotype, 0911–1050 (UFES).

Occurrence: Baltic amber, coast of Baltic Sea, Oligocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Vertex crest convex, without a series of long bristly hairs. Pronotal disc very short. Notauli absent. Propodeal disc with median longitudinal carina incomplete.

Description of the female: Holotype, female, body length 2.0 mm, LFW 1.3 mm. Head. – Head subquadrate in dorsal view, longer than wide. Maxillar palpus with six palpomeres. Clypeus with median clypeal lobe angulate, straight in profile. First five antennal segments in ratio of about 7:3:2:2:2. Eye not gibbous, glabrous. HE 0.45 x LH. VOL 0.7 x HE.
Mesosoma. – Pronotal disc coriaceous, 0.3 x as long as wide, very short, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially; shorter

than the mesoscutum. Mesoscutum 0.5 x as long as wide, coriaceous. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed. Propodeal disc with median longitudinal carina incomplete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subtriangulate. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.23 x LFW. M vein straight. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* straight. Distal margin of Rs*c* convex, ending gently toward anterior margin of forewing. RS+M vein 1.0 x Rs*a*. M vein 2.5 x Rs*a*. Cu*a* vein 2.5 x Rs*a*. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved.

Metasoma. – 3.0 x longer than wide.

Description of male: Allotype, male, body length 1.7 mm, LFW 1.1 mm. Head. – Head subquadrate in dorsal view, longer than wide. Clypeus with median clypeal lobe angulate. First five antennal segments in ratio of about 7:2:2:2:2. Eye not gibbous, small, ≤ 0.5 x LH, glabrous. Ocelli large, > 0.30 x WOT, 0.33 x WOT. HE 0.4 x LH. WH 0.8 x LH. WF 0.6 x WH. WF 1.2 x HE. OOL 3.3 x WOT. VOL 0.7 x HE. Vertex crest 8.0 x DAO. DAO 0.1 x WF. Distance between posterior ocelli 3.0 x DAO. Ocellar triangle compact. Anterior ocellus not surpassing imaginary top eye line. Vertex crest convex.

Mesosoma. – Pronotal disc coriaceous, 0.3 x as long as wide, very short, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially; shorter than the mesoscutum. Mesoscutum 0.4 x as long as wide, coriaceous. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed. Propodeal disc with median longitudinal carina incomplete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subquadrate. 1R1 cell present, 1R1 cell 0.88 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.28 x LFW. M vein straight. Rs*a* slightly diagonal to anterior margin of forewing. Rs*b* straight. Distal margin of Rs*c* convex, ending gently toward anterior margin of forewing. RS+M vein 1.0 x Rs*a*. M vein 1.5 x Rs*a*. Cu*a* vein 2.0 x Rs*a*. Rs*a* slightly inclined toward tegula. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved.

Metasoma. – 2.4 x longer than wide.

Remarks: This species is similar to *Lytopsenella kerneggeri* OHL (Figs. 30-32) in having the notauli absent, the propodeal disc with the median longitudinal carina present but incomplete,

the C cell widening distally, and the second section of the Rs vein (Rs*b*) straight. However, *Lytopsenella maritima* RAMOS & AZEVEDO sp. nov. has a median clypeal lobe with the median carina angulate in profile and the vertex crest convex and lacking long bristly hairs, whereas *L. kerneggeri* OHL has a median clypeal lobe with the median carina strongly arched in profile and the vertex crest straight and bearing a series of long bristly hairs. The fossil record of Bethylinae has hitherto included only female specimens. However, both male and female specimens of *L. maritima* RAMOS & AZEVEDO sp. nov. are known. Thus, this report constitutes the first record of sexual association in fossil species of Bethylinae. The sexual dimorphism is weak in this species, and the specimens share several features indicating that they are conspecific. The male and female specimens have the vertex crest convex, the pronotal disc short, the mesoscutum lacking notauli, the propodeal disc with the median longitudinal carina present but incomplete, the prostigma large and trapezoidal, the Rs*b* of the forewing straight, the Rs*c* of the forewing convex and tapering gently toward the anterior margin of forewing, and the RS+M vein equal to the first section of the Rs vein (Rs*a*). The main differences between the male and female specimens are that the females are slightly larger than the males, the M and Cu veins of the forewing are longer in females, and the 1M cell is triangulate in females but quadrate in males. Considering this evidence, we are convinced that these specimens represent conspecific female and male *L. maritima* RAMOS & AZEVEDO sp. nov.

Genus *Sierola* CAMERON, 1881

Type species: *Sierola testaceipes* CAMERON, by monotypy.

Sierola rovniana RAMOS & AZEVEDO sp. nov.

Figs. 51-53

Etymology: The specific epithet *rovniana* is in allusion to the Rovno region of the Ukraine.

Material examined: Holotype. Ukraine, Klesov, Rovno amber, 1 female, nº K-24208 (SIZK).

Occurrence: Rovno amber, Ukraine, Upper Eocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight. Notaulus present. Forewing with first medial cell closed, and nebulous. 1R1 cell absent. C cell evenly narrow. 2R1cell closed, and subtriangulate. Distal margin of Rs*c* ending abruptly toward anterior margin of forewing. R cell formed by nebulous veins. 1Cu cell formed by nebulous veins. 1M cell formed by nebulous veins.

Description: Holotype, female, body length 2.0 mm, LFW 1.2 mm.

Head. – Head subtriangular in dorsal view, as long as wide. Clypeus with median clypeal lobe angulate, with median carina. First five antennal segments in ratio of about 9:3:3:3:3. Eye not gibbous, glabrous. Ocelli small, ≤ 0.30 x WOT, 0.2 x WOT. HE 0.5 x LH. WH 1.0 x LH. WF 0.5 x WH. WF 1.0 x HE. OOL 1.4 x WOT. VOL 0.33 x HE. Vertex crest 5.0 x DAO. DAO 0.1 x WF. Distance between posterior ocelli 5.0 x DAO. Ocellar triangle not compact. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight. Mesosoma. – Pronotal disc coriaceous, 0.66 x as long as wide, posterior margin slightly concave medially. Mesoscutum 0.5 x as long as wide, coriaceous. Notaulus present, convergent posteriorly. Scutellum with scutellar fovea elliptical, wide. Prosternum expanded, excavated medially, excavation complete. Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, but nebulous. 1R1 cell absent. C cell evenly narrow. 2R1 cell closed, subtriangulate, 0.21 x LFW. R cell formed by nebulous veins. 1Cu cell formed by nebulous veins. 1M cell formed by nebulous veins. Distal margin Rs*c* ending abruptly toward anterior margin of forewing. Stigma not expanded, rectangular, distal stigma margin truncate.

Legs. – Profemur 2.2 x longer than wide. Claws bifid, curved.

Metasoma. – 2.4 x longer than wide.

Male unknown.

Remarks: This species is similar to *Sierola hastata* SORG, 1988 in having 13 antennomeres and the 2R1 cell closed and subtriangulate. However, *Sierola rovniana* RAMOS & AZEVEDO sp. nov. has the distal margin of Rs*c* ending abruptly toward the anterior margin of the forewing and the R, 1Cu, and 1M cells formed by nebulous veins, whereas *S. hastata* SORG has the distal margin of Rs*c* tapering gently toward the anterior margin of the forewing and the R, 1Cu, and 1M cells formed by tubular veins.

4. Discussion

No other fossil locality is comparable with Baltic amber in terms of diversity, and its amber inclusions are undoubtedly among those most widely known by lay people. However, Rovno amber has long been considered poor in inclusions, even compared to Belarusian amber (ZHERIKHIN & ESKOV 1999). Today, the Rovno and Belarusian ambers are considered identical, redeposited over a territory encompassing parts of both countries (PERKOVSKY et al. 2007, 2010).

Rovno amber is chemically identical to Baltic amber, and both are considered roughly contemporaneous, dating from the Late Eocene (PERKOVSKY et al. 2007). However, Oise amber is autochthonous and substantially differs from Baltic amber in age (earliest Eocene, 53 My), chemical composition, and origin (NEL et al. 1999).

In general, fossil evidence is necessary to accurately understand the character combinations found in living species. Thus, the material analyzed here may allow us to further study the evolution of the characters preserved in the Bethylinae specimens.

Lytopsenella KIEFFER includes four fossil species from Baltic amber (Upper Eocene): *L. crastina*, *L. setigera*, and *L. simplex*, described by BRUES (1923), and *L. kerneggeri*, described by OHL (1995) (Figs. 33-44). Thus, *Lytopsenella* is the genus of Bethylinae with the largest number of described fossil species. The known distribution and taxonomic variation of *L. kerneggeri* OHL are here expanded: this species is recorded for the first time from Rovno amber. *Lytopsenella* closely resembles *Eupsenella*, mainly differing in having the 2R1 cell clearly longer. In *Lytopsenella*, the 1R1 cell of the forewing is always significantly shorter than the 2R1 cell; in *Eupsenella*, the 1R1 cell is equal to or longer than the 2R1 cell.

In most species of Bethylinae, the veins are tubular. However, *Sierola rovniana* RAMOS & AZEVEDO sp. nov. (Figs. 51, 53) exhibits a novel pattern. In this species, the R, 1Cu, and 1M cells are wholly formed by nebulous veins. The only cell in the forewing formed by tubular veins is the 2R1 cell, whereas in *Sierola hastate* Sorg, 1988, for example, the R, 1Cu, and 1M cells are formed by tubular veins. This peculiarity of *S. rovniana* Ramos & Azevedo sp. nov. is new for this genus.

Several aspects of *Eupsenella* are notable. The fossil *Eupsenella* species analyzed here closely resemble the living species, although the 2R1 cell appears consistently longer in the fossil species.

WESTWOOD (1874) cited five to six apical mandibular teeth in the original description of the genus, but all living species have four apical mandibular teeth (see RAMOS & AZEVEDO 2012). This condition also appears in *E. aulax* RAMOS & AZEVEDO sp. nov. (Figs. 5, 10) and *E. rossica* RAMOS & AZEVEDO sp. nov. (Fig. 20). However, it was not possible to count the exact number of apical teeth in *E. klesoviana* RAMOS & AZEVEDO sp. nov. and *E. yantarnica* RAMOS & AZEVEDO sp. nov. because the mandible was not clearly discernible.

The pronotal disc is usually simple in *Eupsenella*. However, a novel pattern occurs in *E. aulax* RAMOS & AZEVEDO sp. nov. (Figs. 5-6, 9). This species has a peculiar deep transverse furrow near the posterior margin. This character is completely new for *Eupsenella.*

According to RAMOS & AZEVEDO (2012), the prosternum is clearly expanded in *Eupsenella*. This character appears in all fossil *Eupsenella* species analyzed here, including *Eupsenella eocenica* (DE PLOËG & NEL, 2004) comb. nov. (Fig. 2).

In extant *Eupsenella* species the notauli are always evenly narrow. However, a novel pattern appears in *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. (Figs. 24, 27), which has the notauli strongly widened posterad.

Characters related to wing venation are especially useful for delimiting living and fossil *Eupsenella* species. No new pattern was found in this study. Notably, however, the 2R1 cell of the forewing is never longer than the 1R1 cell in extant *Eupsenella* species; at most, the 2R1 cell is equal to the 1R1 cell. All fossil *Eupsenella* species described here have the 2R1 cell as long as the 1R1 cell, corroborating the proposed pattern for *Eupsenella*.

Regarding the geographical distribution of the genus, extant *Eupsenella* species are restricted to Australia, except for *E. insulana* GORDH & HARRIS, 1996, which also occurs in New Zealand. Thus, the distribution of *Eupsenella* has hitherto been confined to the Australian region. However, we here describe two new species from Ukraine, *E. aulax* RAMOS & AZEVEDO sp. nov. (Figs. 5-9) and *E. klesoviana* RAMOS & AZEVEDO sp. nov. (Rovno amber) (Figs. 13-16), and two new species from Russia, *E. rossica* RAMOS & AZEVEDO sp. nov. (Figs. 17-22) and *E. yantarnica* RAMOS & AZEVEDO sp. nov. (Baltic amber) (Figs. 23-27). Thus, this genus had a much wider geographical distribution in the past. This information demonstrates that *Eupsenella* species were present outside the Australian region between 36 and 37 My. *Eupsenella* thus provides a further example of a group whose contemporary distribution is southern ("Gondwanan") but that is present in the fossil record of northern continents, indicating a formerly global distribution (ESKOV 2002).

However, extant species of the genus *Goniozus* Förster are present worldwide, recorded from the Oriental, Neotropical, Nearctic, Palearctic, Afrotropical, and Australian regions. According to Lim & Lee (2012), *Goniozus* comprises approximately 170 species. However, only two fossil species have been described previously: *Goniozus contractus* (BRUES, 1933) from Baltic amber (Eocene) and *Goniozus respectus* SORG, 1988 from Dominican amber (Miocene). Here, a third fossil *Goniozus* species is described: *G. definitus* RAMOS & AZEVEDO sp. nov. (Figs. 28-32) from Baltic amber.

Wing venation is also important for delimiting modern and fossil *Goniozus* species. Species of this genus can have the 1M cell (areolet) of the forewing either closed or open (see Polaszek & Krombein 1994). In *G. definitus* RAMOS & AZEVEDO sp. nov., *G. contractus*, and *G. respectus*, the forewing 1M cell is closed. This character occurs in most *Goniozus* species. In several species, however, the areolet is incomplete; only the upper part is preserved as a 'stub' arising from the Rs*a* vein. This character occurs, for example, in *G. floridanus* (ASHMEAD).

Considering that the types of most fossil species of Bethylinae have been lost, except those of *L. kerneggeri* and *E. eocenica* (see above), the present study is important because it confirms information previously available only in the literature.

Cenozoic ambers preserve 17 species in five genera of Bethylinae (Table 1). *Lytopsenella* and *Eupsenella*, the two genera with the most complete wing venation known in the subfamily, predominate, as expected for this ancient fauna. The material examined in the present study consists of 12 specimens representing as many as nine species and four genera. This small number of specimens per species suggests a comparatively high diversity and low abundance of bethyline wasps visiting amber trees. In our material, two species are known from two specimens each: *L. kerneggeri* and *L. maritima*. The two specimens of the former species come from two different kinds of amber (Baltic and Rovno), suggesting that the source areas of these two ambers were similar in their fauna despite their geographical separation (DLUSSKY & RASNITSYN 2009; PERKOVSKY et al. 2010). The Cenozoic bethyline fauna was generally uniform across time and space, at least at the generic level: both older (Oise) and younger (Dominican) ambers, which are found at almost opposite points of the globe, reveal the same genera known from the Baltic and Rovno ambers (*Eupsenella* and *Goniozus*). Nevertheless, the generic composition of local amber assemblages displays non-trivial differences; for example, *Sierola* occurs in both the Rovno and Danish ambers but not in the much better-explored Baltic amber. A similar case has been reported for the ant genus

Fallomyrma DLUSSKY & RADCHENKO, 2006 (PERKOVSKY & RASNITSYN 2013). This observation has been interpreted to indicate similarity between the environments and climatic conditions of the Rovno and Danish amber source areas in contrast to that of the Baltic amber (DLUSSKY & RASNITSYN 2009; PERKOVSKY 2011). The distribution of *Sierola* further supports this inference.

Our findings include other notable observations. For example, SORG (1988) considered Bethylinae to be basal within Bethylidae (excluding unplaced genera such as *Cretobethylellus*, some of which might be even more basal). However, all known genera of this subfamily are still living; not one is extinct. This pattern is rather uncommon and suggests that more ancient and diverse assemblages of Bethylinae, including extinct genera, remain unknown.

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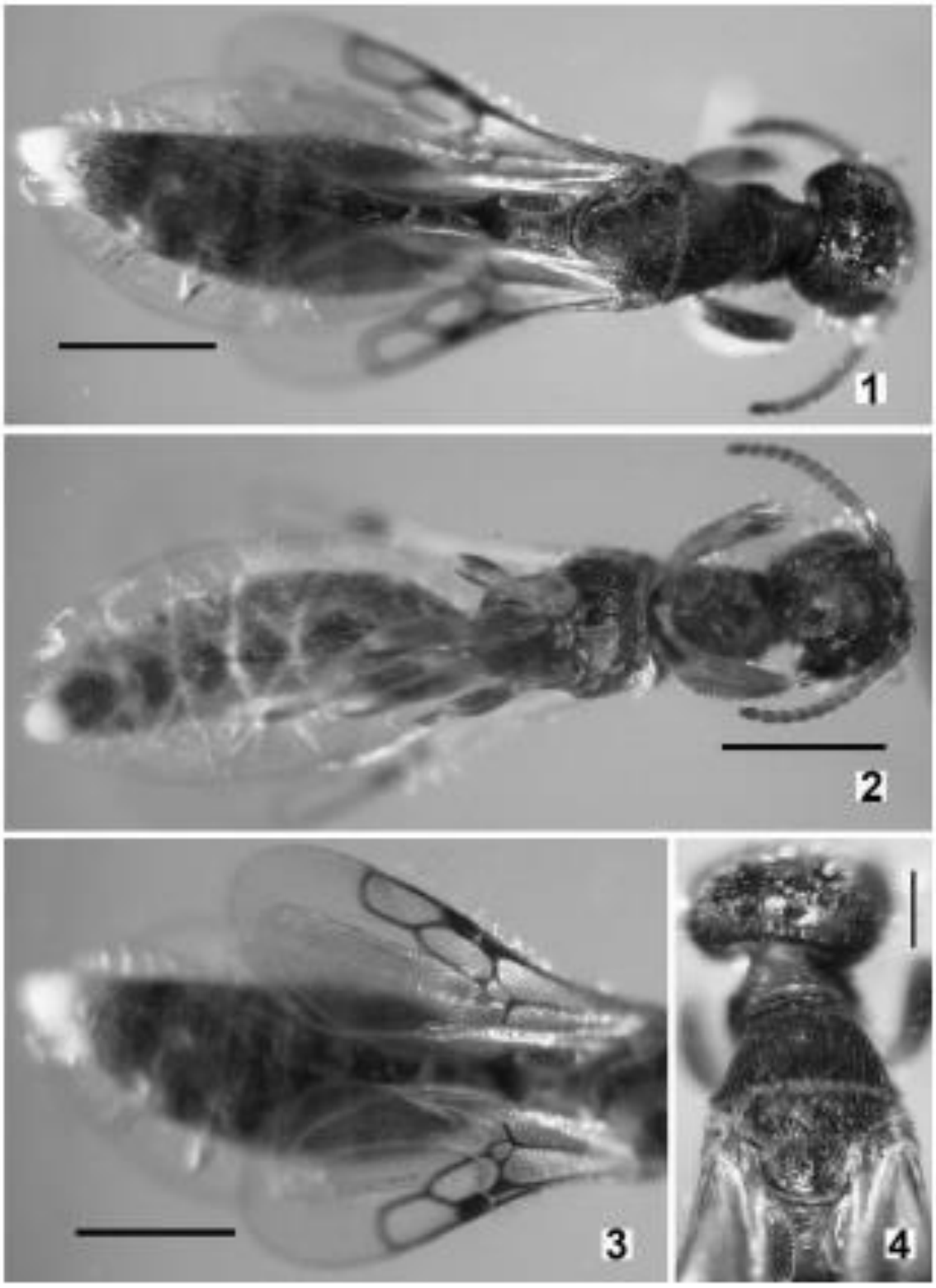

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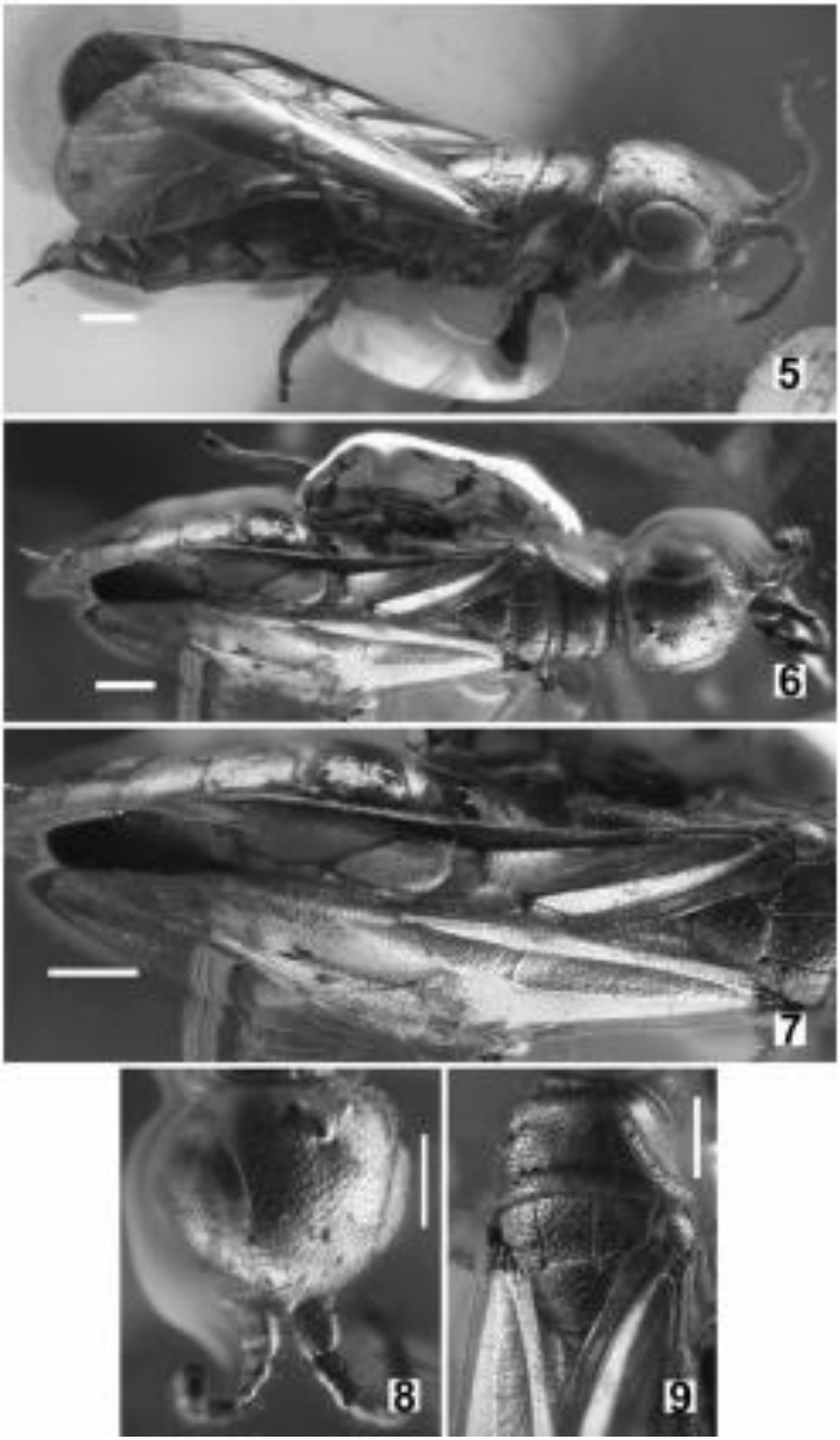

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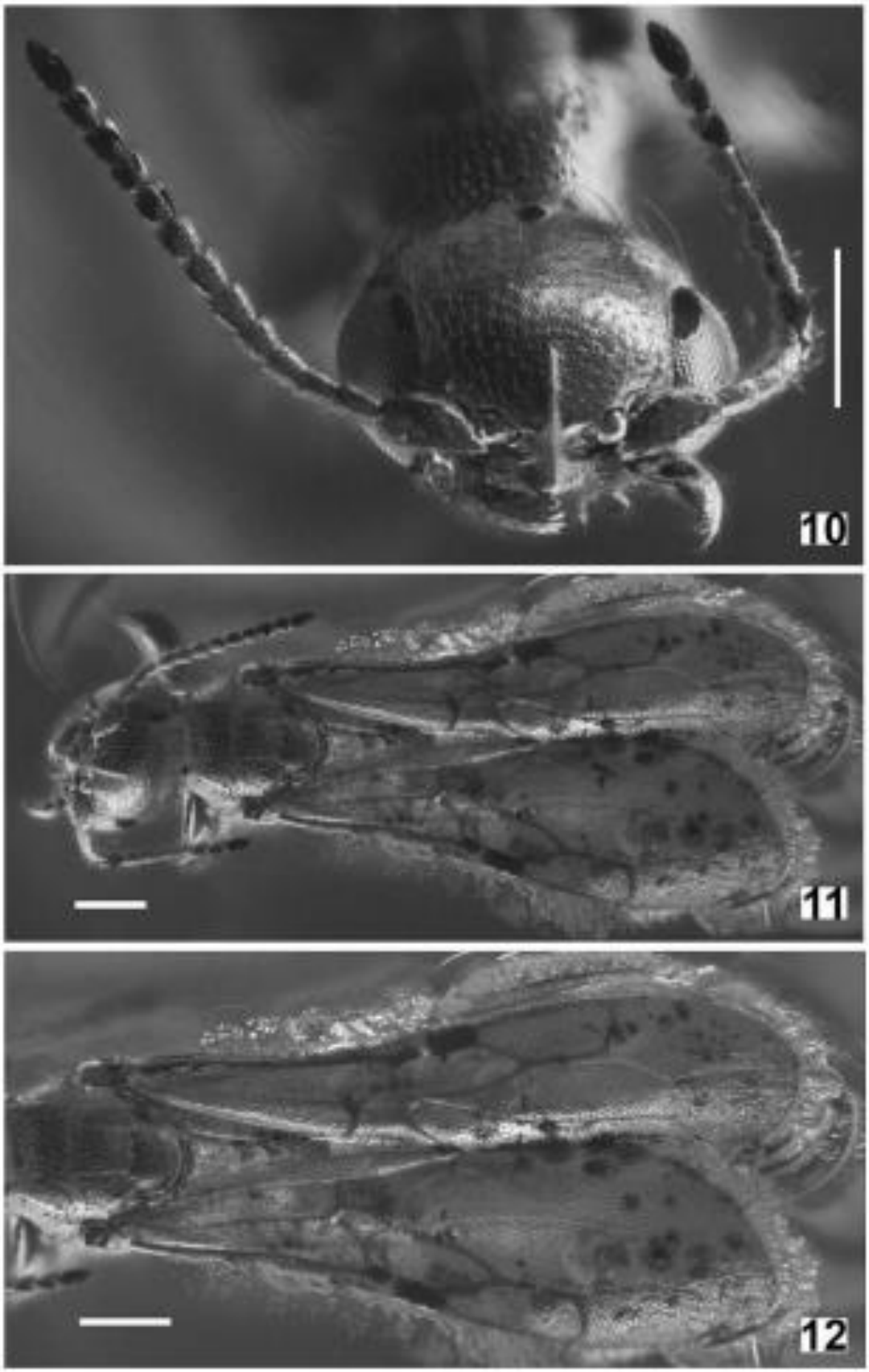

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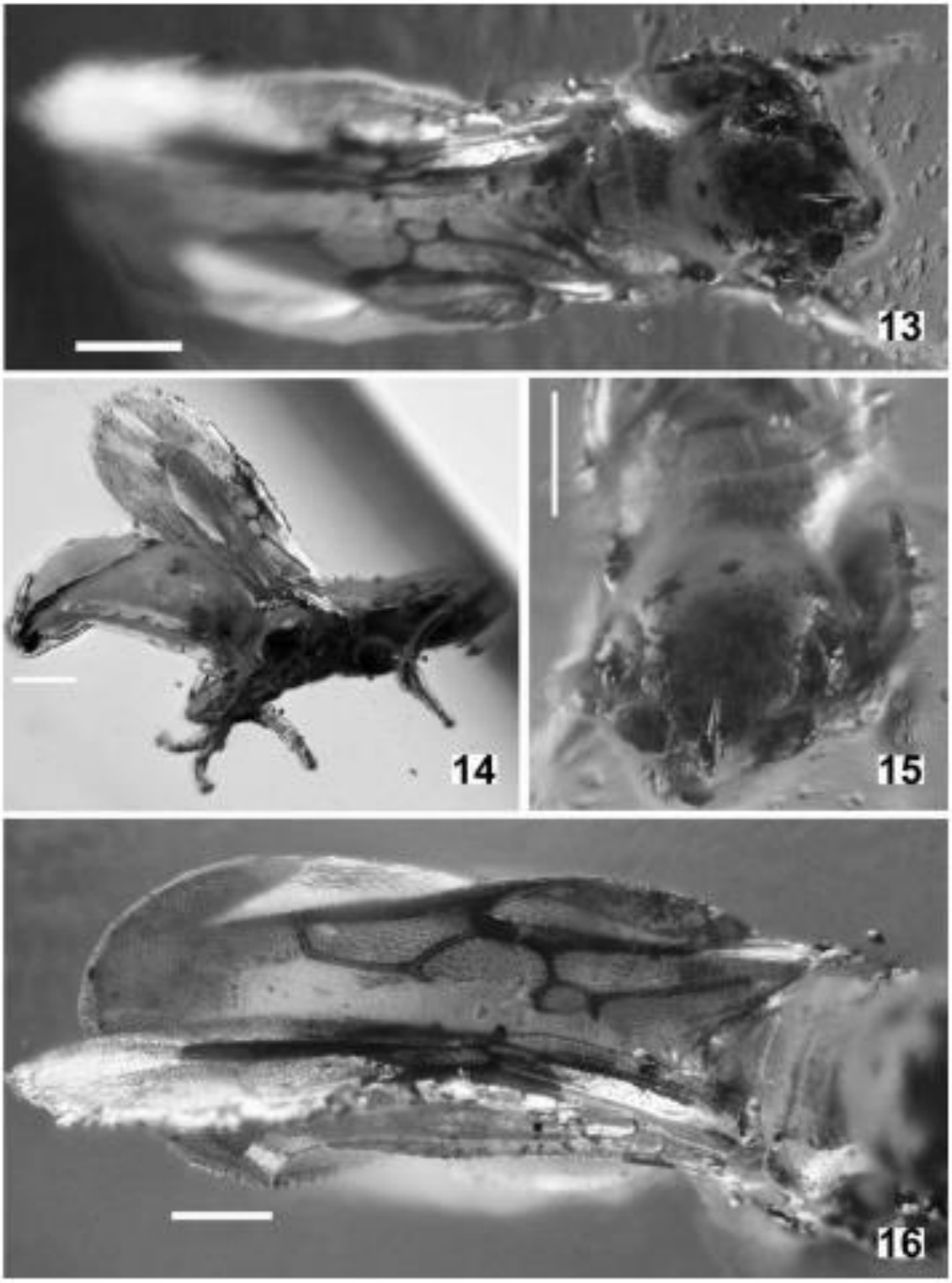

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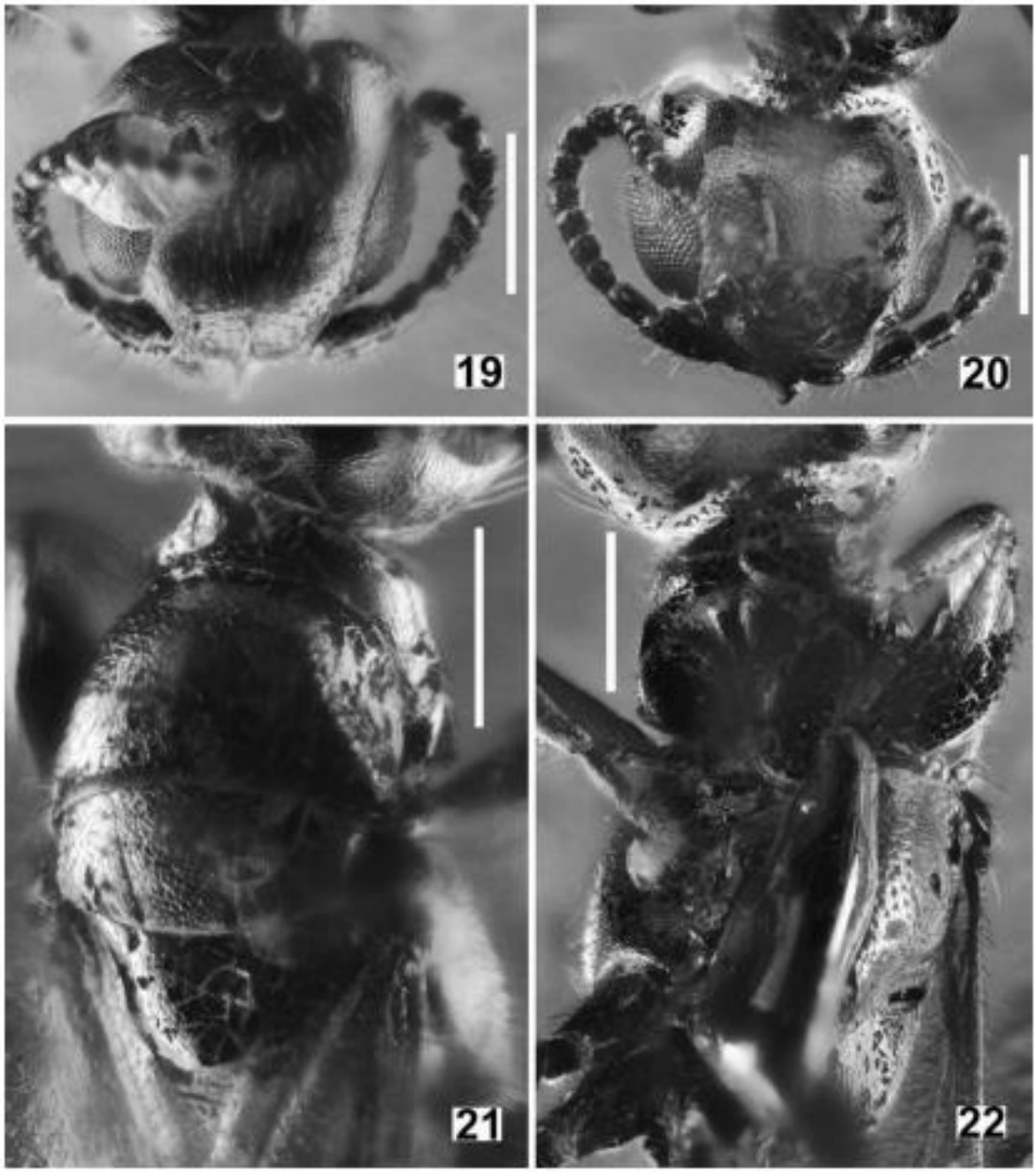

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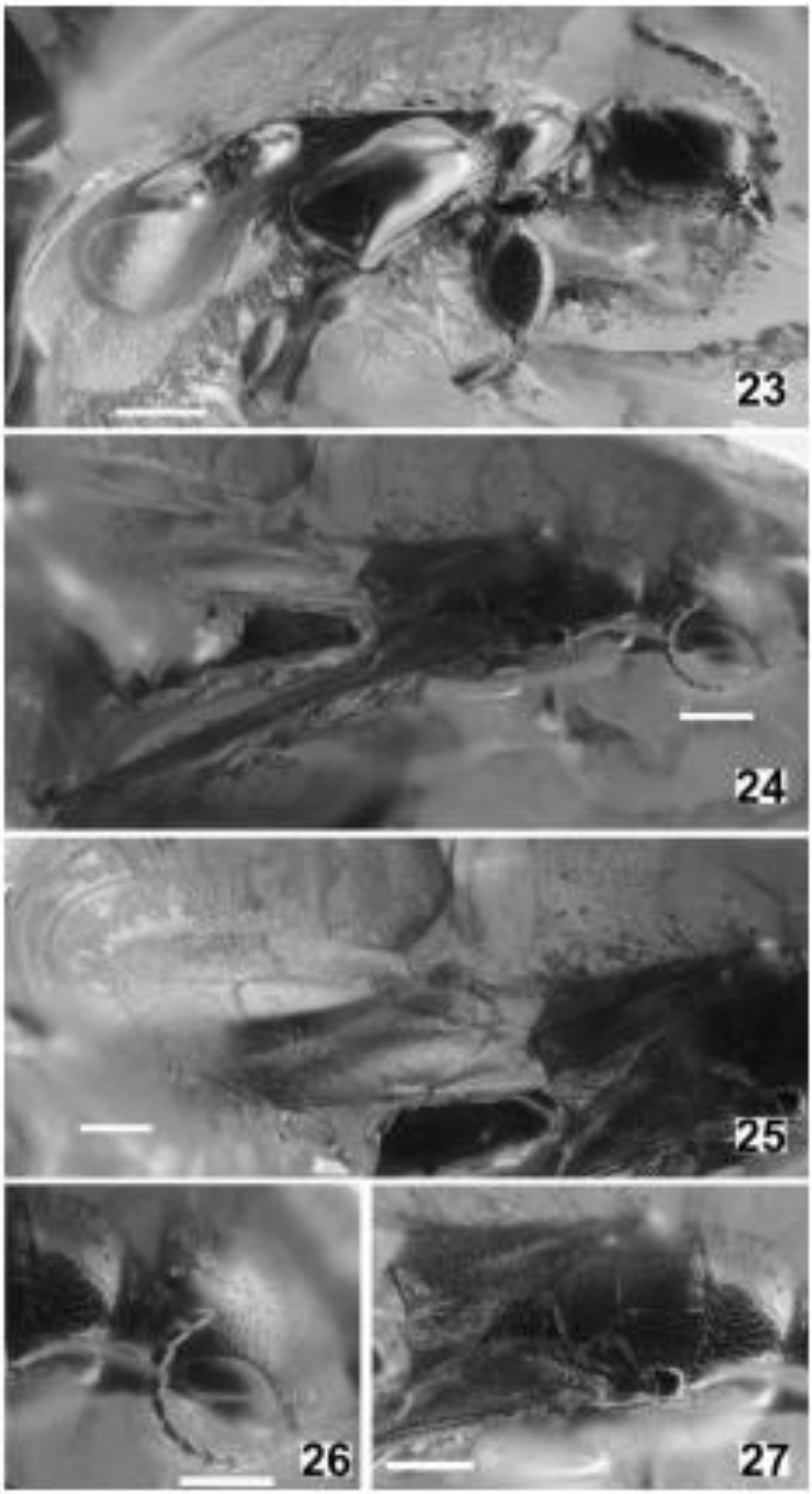

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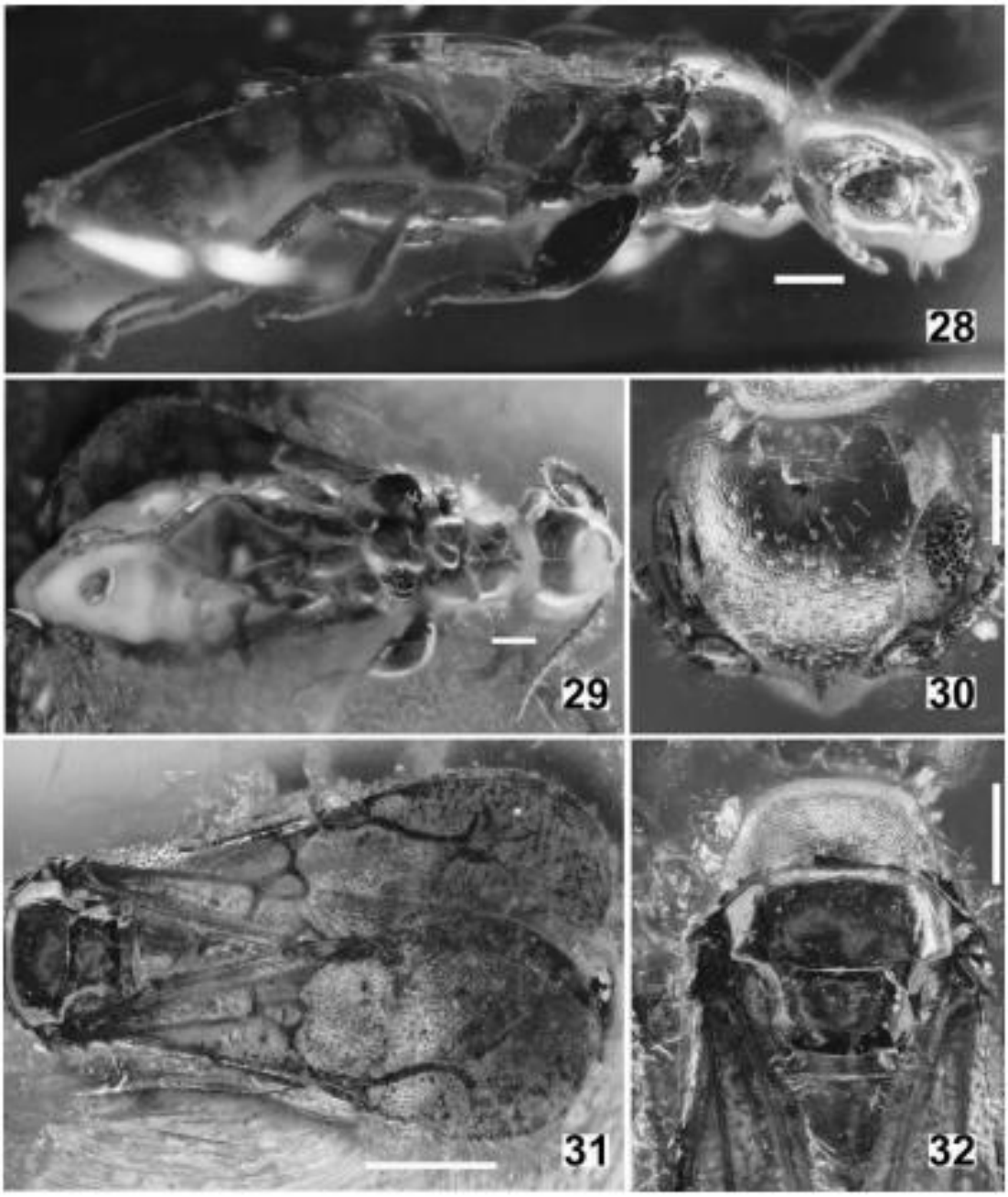

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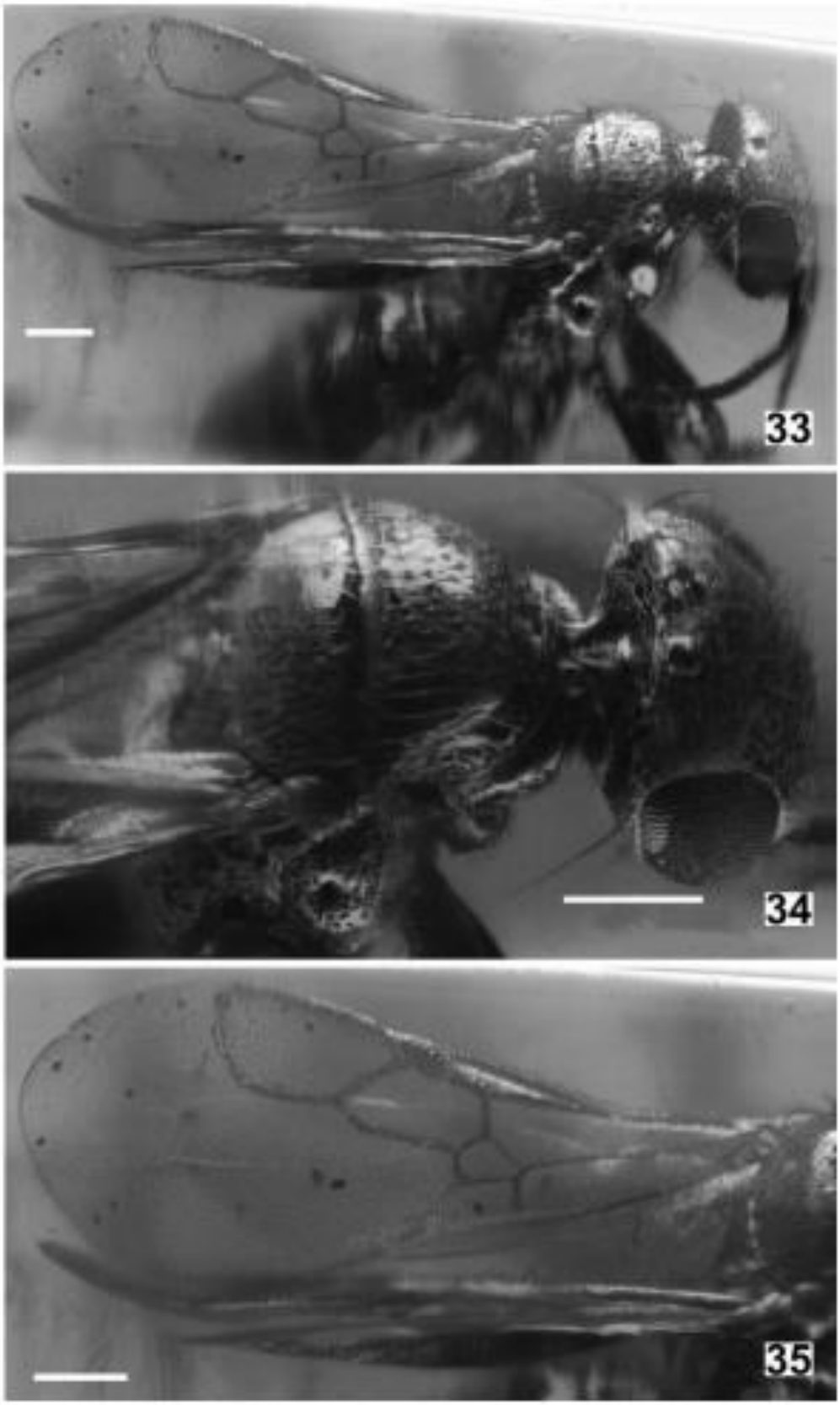

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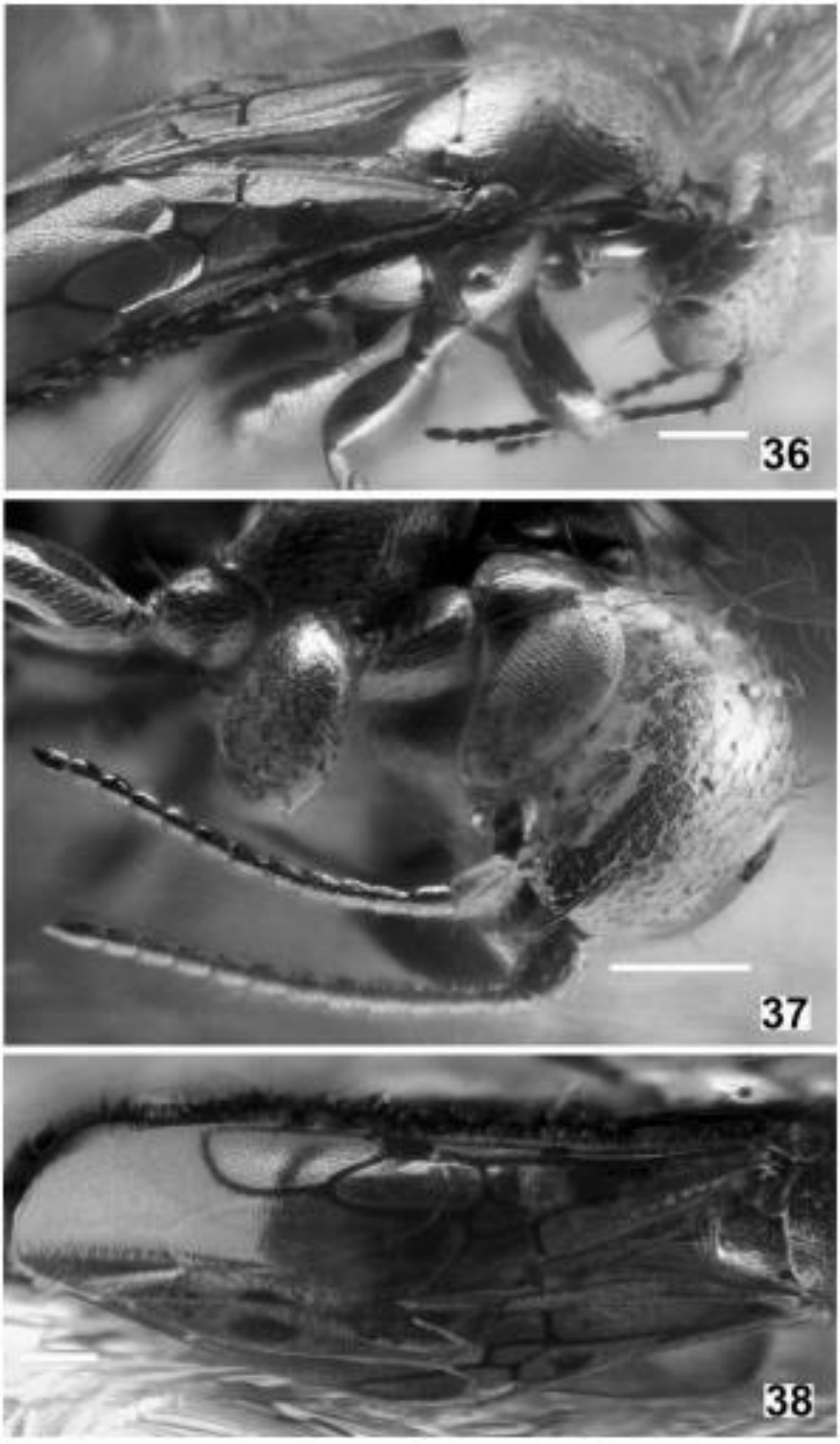

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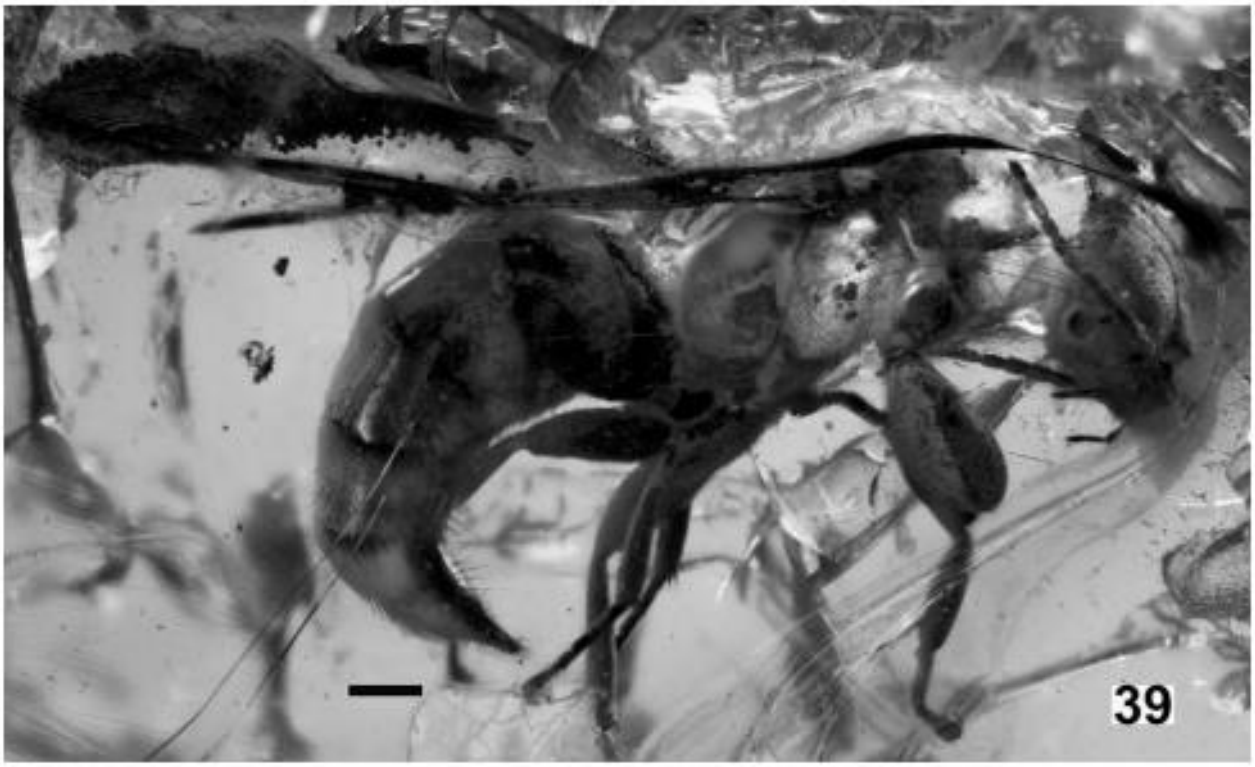

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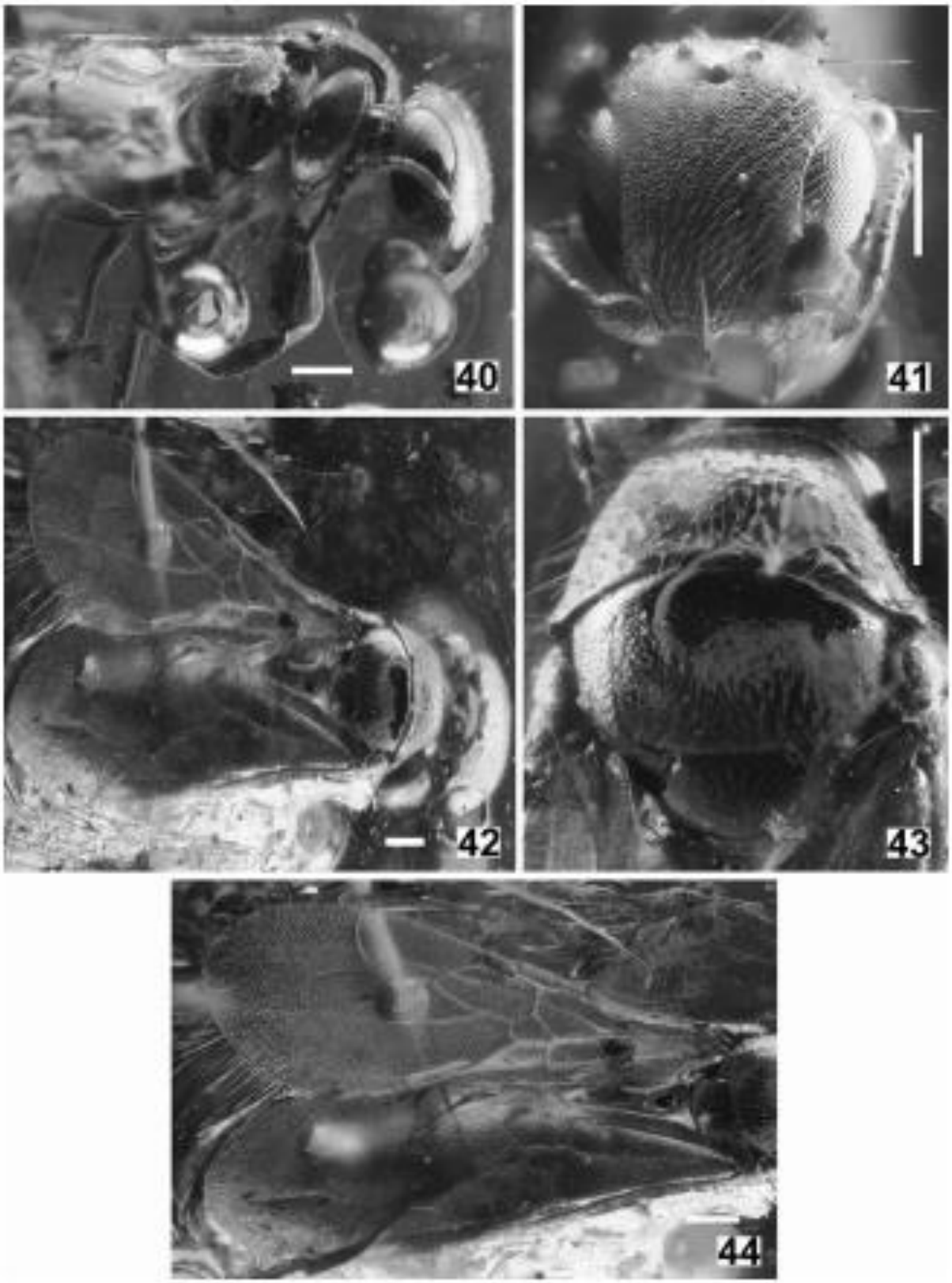

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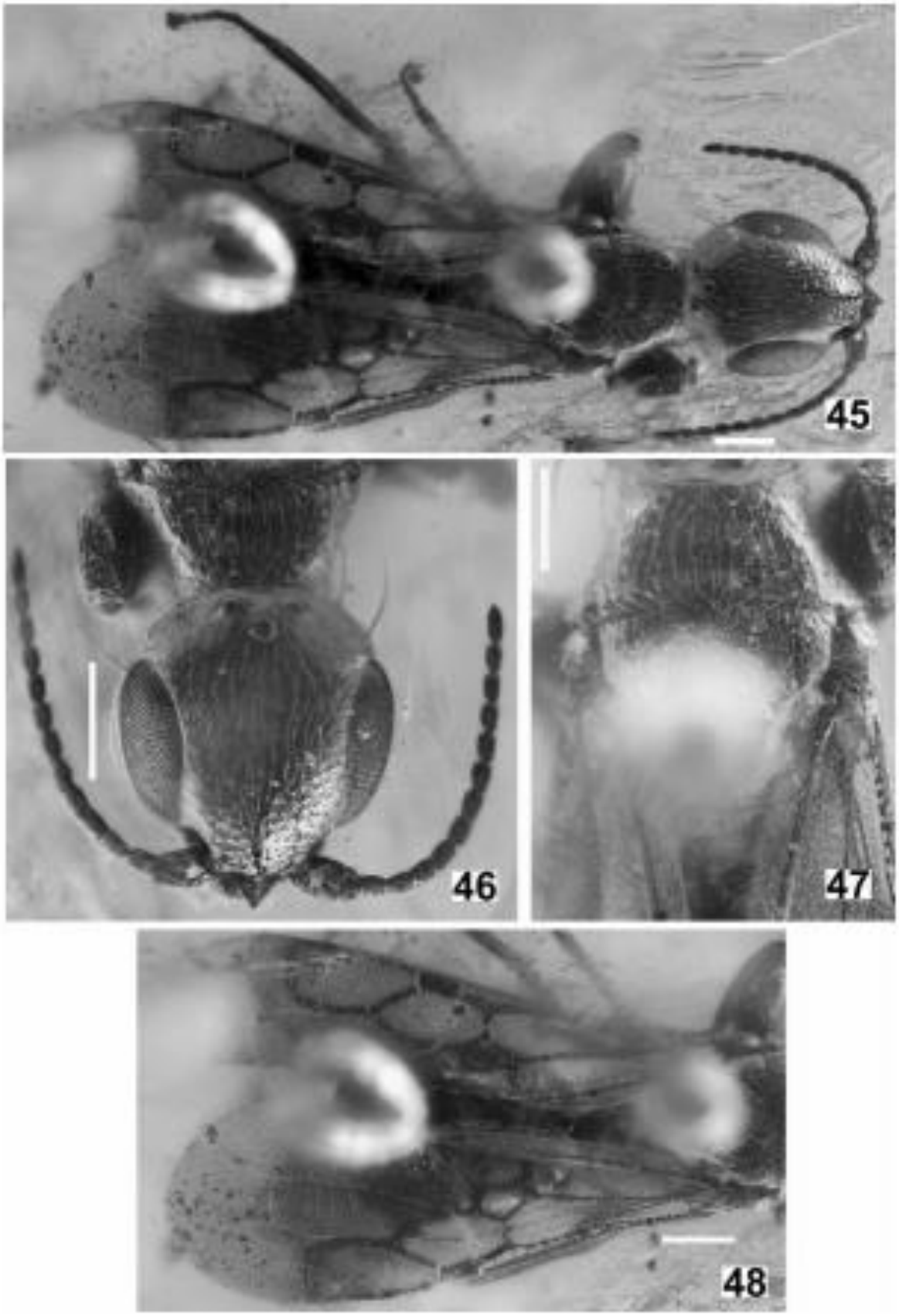

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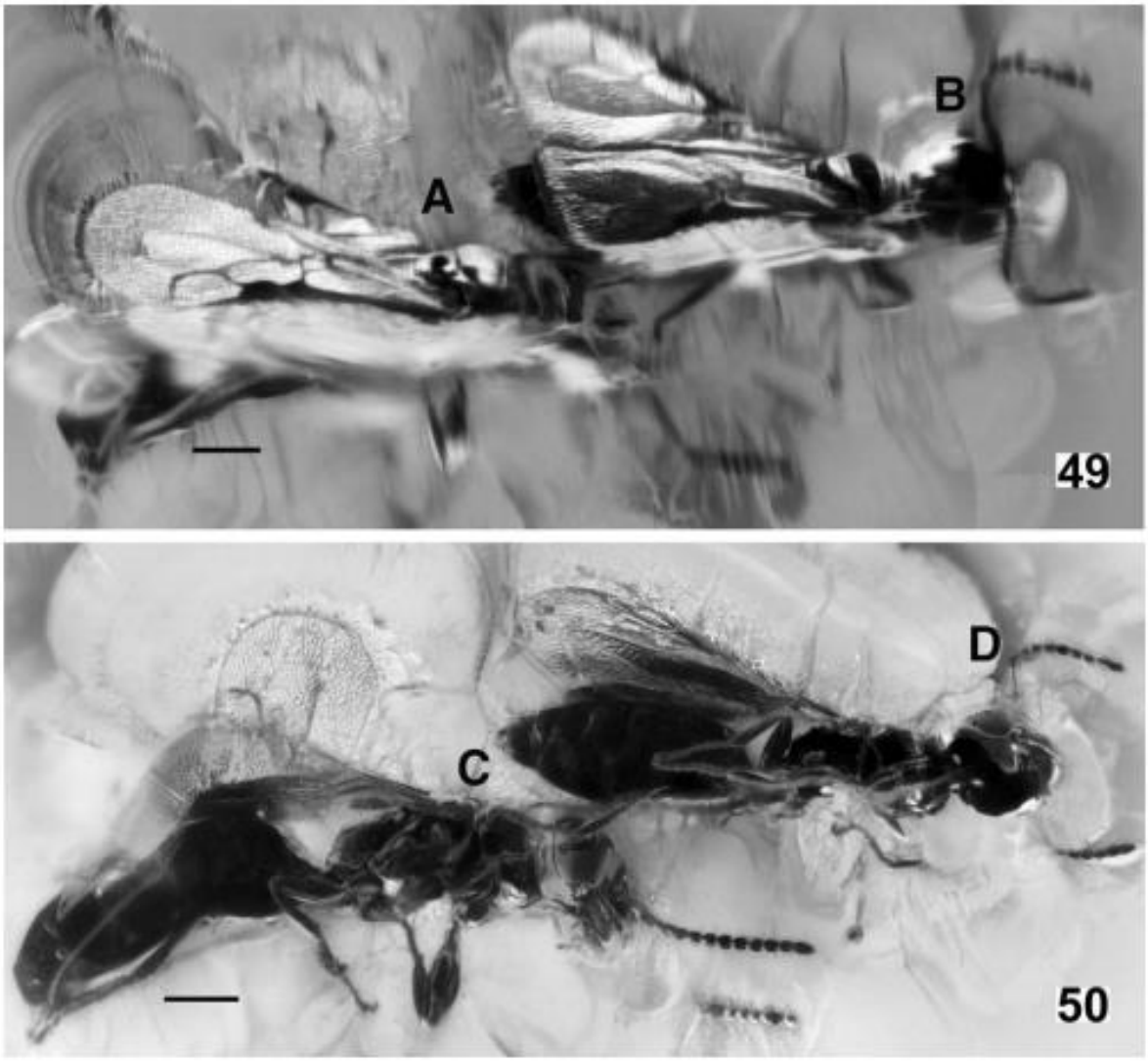

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Table 1. Valid species of fossil Bethylinae.

Taxon	Age	Amber	References
Eupsenella aulax RAMOS & AZEVEDO sp. nov.	Late Eocene	Rovno	This paper
Eupsenella klesoviana RAMOS & AZEVEDO sp. nov.	Late Eocene	Rovno	This paper
Eupsenella eocenica (DE PLOËG & NEL, 2004) comb. nov.	earliest Eocene	Oise	DE PLOËG & NEL (2004), this paper
Eupsenella rossica RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
Eupsenella yantarnica RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
Goniozus contractus (BRUES, 1933)	Late Eocene	Baltic	BRUES (1933)
Goniozus respectus SORG, 1988	Middle Miocene	Dominican	SORG (1988)
Goniozus definitus RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
Lytopsenella crastina (BRUES, 1923)	Late Eocene	Baltic	BRUES (1933)
Lytopsenella setigera (BRUES, 1923)	Late Eocene	Baltic	BRUES (1933)
Lytopsenella simplex (BRUES, 1923)	Late Eocene	Baltic	BRUES (1933)
Lytopsenella kerneggeri OHL, 1995	Late Eocene	Baltic & Rovno	OHL (1995), this paper
Lytopsenella baltica RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
Lytopsenella maritima RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
Prosierola submersa BRUES, 1933	Late Eocene	Baltic	BRUES (1933)
Sierola hastata SORG, 1988	Late Eocene	Danish	SORG (1988)
Sierola rovniana RAMOS & AZEVEDO sp. nov.	Late Eocene	Rovno	This paper

CÁPITULO 2

AFROBETHYLUS RAMOS & AZEVEDO, GEN. NOV., A NEW REMARKABLE AFROTROPICAL GENUS OF BETHYLINAE (HYMENOPTERA: BETHYLIDAE)

Abstract

Afrobethylus Ramos & Azevedo, **gen. nov.** (type species *Afrobethylus zulu* Ramos & Azevedo, **sp. nov.**) with six new species, *Afrobethylus antankarana* Ramos & Azevedo, **sp. nov.** (Madagascar), *A. antemoro* Ramos & Azevedo, **sp. nov.** (Madagascar), *A. bapedi* Ramos & Azevedo, **sp. nov.** (South Africa), *A. swazi* Ramos & Azevedo, **sp. nov.** (South Africa), *A. vezo* Ramos & Azevedo, **sp. nov.** (Madagascar), A. *zulu* Ramos & Azevedo **sp. nov.** (South Africa) are described and illustrated. This genus is characterized by having the antenna with ten flagellomeres; the forewing with second radial cell closed; the female genitalia with dorsal ramus of second valvula broadly enlarged, and the presence of proximal projection starting from the base of second valvifer. A key to the species of *Afrobethylus* based on females is provided.

Key words: Chrysidoidea, systematics, female genitalia, Africa

Introduction

While sorting hundreds of samples of Bethylidae material collected in Madagascar under the scope of the project "Terrestrial Arthropod Inventory of Madagascar" coordinated by Brian Fisher and in South Africa under the scope of "Afrotropical Hymenoptera Initiative" coordinated by Simon van Noort, some specimens of Bethylinae pushed our attention. They have an unusual combination of characters never seen before. They have the antenna with ten flagellomeres as in *Bethylus* Latreille, but also have the forewing with second radial cell closed as in Sierola Cameron. Such combination does not correspond to any of the seven valid genera of Bethylinae, so that it represents a new genus.

The main goal of this paper is to recognize, define and describe this new genus, its new species. In addition, to define the diagnostic characteristics of the new genus, *Afrobethylus* **gen. nov.**, as well as provide a key to species of Afrotropical region based on females.

Material and methods

The material was provided by CASC, California Academy of Sciences (Robert Zuparko) and ISAM, Iziko South Africa Museum (Simon van Noort).

The terms of body structures, measurements and indices used in this study follows Azevedo (1999), Evans (1964), and Kawada et al. (2015).

The integument sculpture follows Harris (1979). The nomenclature of wings follows Ramos & Azevedo (2012). The measurements used in this study are as follows: body length from the apex of clypeus to the posterior margin of the last metasomal segment, excluding the female sting; length of forewing in dorsal view; maximum length of antenna; ratio of the first five antennal segments; length of metasoma; ratio of the maximum length and maximum width; ratio of length of second valvula and ratio of maximum length of the second valvula by maximum length of the first valvula; length of sting; ratio of maximum length of sting and maximum length of body of genitalia.

The terminology used by female genitalia follows the Hymenoptera Anatomy Ontology (HAO) project (Yoder et al. 2010, Seltmann et al. 2012). The anatomical terms used in the descriptions of this structure follow HAO at Hymenoptera Anatomy Portal (http://portal.hymao.org), and are as follow: (1vv) first valvula; (2vv) second valvula; (3vv) third valvula; (1vf) first valvifer; (2vf) second valvifer; (vr1) ventral ramus of first valvula; (vr2) ventral ramus of the second valvula; (Fu) furcula, (d1vf) dorsal sclerite of the first valvifer; (pp2vf) proximal projection starting from the base of second valvifer ; and (iav) intervalvifer articulation.

The taxa considered in this paper are distributed within the Afrotropical region. This is defined by Crosskey and White (1977) to include Africa south of the Sahara Desert, conveniently delimited by the 254 mm (10 inches) rainfall isohytes, and the Malagasy region.

The descriptions and key were elaborated with DELTA (Descriptive Language for Taxonomy) according to Dallwitz et al. (1993).

Images were obtained using Leica MD2500 Microscope magnifying glass attached to a Leica DFC 495 video camera captured using Leica LAS (Leica Application Suite V3.6.0) Microsystems by Leica (Switzerland) Limited and combined using HELICON FOCUS (version 4.2.9): render method based on Method C (Pyramid). All illustrations and plates were edited in a software for edition of images and vectorization using the adjustments (e.g., levels, shadows/highlights), tools (e.g., healing brush, clone stamp) and filters (e.g., unsharp mask), respectively.

All specific epithets of the new species are names or collective designations of African ethnic groups.

***Afrobethylus* Ramos & Azevedo, gen. nov.**

(Figs 1A–G)

Diagnosis. Antenna with 10 flagellomeres. Notaulus absent. Metapectal-propodeal complex without median longitudinal carina; metapostnotal-propodeal suture inconspicuous; posterior transverse carina absent. Fu Vshaped; 1vf large; 2vf large; vr2 broadly enlarged, bifid; pp2vf present, curved.

Description. Female. Head. Mandible with four sharpened apical teeth. Antenna with 10 flagellomeres.

Mesosoma. Notaulus absent. Mesoscutellum with pair of elongate and inclined foveae. Metapectal-propodeal complex coriaceous-punctate; without median longitudinal carina; metapostnotal-propodeal suture inconspicuous; posterior transverse carina absent. Mesopleuron coriaceous-punctate; mesopleural pit shallow. Prosternum large, excavated medially. Forewing. Costal cell conspicuous only apically; second radial cell closed, long, triangular; Rs vein shorter than M vein; stigma well developed. Legs. Profemur expanded. Tarsal claws bifid, strongly curved.

Genitalia. Fu V-shaped; 1vf large; vr1 large; 2vf large; vr2 broadly enlarged, bifid; d1vf thorn shaped; pp2vf present, curved; distal region of the sting tapering abruptly; 3vv wide, and long.

Male. unknown.

Type-species. *Afrobethylus zulu* Ramos & Azevedo, **sp. nov.**

Species included. *Afrobethylus antankarana* Ramos & Azevedo, **sp. nov.**, *A. antemoro* Ramos & Azevedo, **sp. nov.**, *A. bapedi* Ramos & Azevedo, **sp. nov.**, *A. swazi* Ramos & Azevedo, **sp. nov.**, *A. vezo* Ramos & Azevedo, **sp. nov.**, *A. zulu* Ramos & Azevedo, **sp. nov.**

Remarks. This genus is easily recognizable among the other genera of Bethylinae by having the unique combination of antenna with ten flagellomeres and the forewing with second radial cell closed.

Etymology. The name *Afrobethylus* is an allusion to the names “Africa”, continent from the specimen was collected, and the name “Bethylus” the type genus of Bethylinae.

Key to species for females of *Afrobethylus* (males unkown)

1. Eye glabrous (Figs 2B, 3B, 4B, 5B, 6B); genitalia with pp2vf of 2vf long (Figs 2C, 3C, 4C, 5C, 6C) 2

- Eye with sparse pilosity (Fig. 7B); genitalia with pp2vf of 2vf short, and wide (Fig. 7C)……...*A. zulu* Ramos & Azevedo, **sp. nov.**

2(1). Forewing with flexion lines forming rectangular area, when present delimited by three flexion lines (Figs 3A, 4A)…….3

- Forewing with flexion lines not forming rectangular area, when present only one longitudinal flexion line (Figs 2A, 4A, 5A)…….....4

3(2). Ocelli small (Fig. 3B); median clypeal lobe rounded (Fig. 3B); sting (1vv+2vv) as long as body of genitalia (Fig. 3C); genitalia with 2vv as long as to 1vv (Fig. 3C).....*A. antemoro* Ramos & Azevedo, **sp. nov.**

- Ocelli large (Fig. 6B); median clypeal lobe angled (Fig. 6B); sting (1vv+2vv) longer than body of genitalia (Fig. 6C), genitalia with 2vv shorter than 1vv (Fig. 6C)…..*A. vezo* Ramos & Azevedo, **sp. nov.**

4(2). Head with vertex crest convex (Figs 2B, 4B); forewing with distal margin of 2R1 cell forming right angle (Figs 2A, 4A); sting (1vv+2vv) as long as body of genitalia (Figs 2C, 4C); genitalia with 2vv as long as to 1vv (Figs 2C, 4C)…….5

- Head with vertex crest straight (Fig. 5B); forewing with distal margin of 2R1 cell not forming right angle (Fig. 5C); sting (1vv+2vv) longer than body of genitalia (Fig. 5C); genitalia with 2vv shorter than 1vv (Fig. 5C)……*A. swazi* Ramos & Azevedo, **sp. nov.**

5(4). Median clypeal lobe angled (Fig. 4B); median clypeal carina present; head with area between anterior margin of eye and demarcation of median clypeal lobe almost straight (Fig. 4B)……*A. bapedi* Ramos & Azevedo, **sp.nov.**

- Median clypeal lobe rounded (Fig. 2B); median clypeal carina absent; area between anterior margin of eye and demarcation of median clypeal lobe clearly concave (Fig. 2B)……*A. antankarana* Ramos & Azevedo, **sp. nov.**

***Afrobethylus antankarana* Ramos & Azevedo, sp. nov.**

(Figs 2A–D)

Description. Holotype. Female. Body length 5.4 mm; forewing 3.14 mm long. Colour. Head dark castaneous, mandible dark castaneous. Mesosoma dark castaneous. Metasoma dark castaneous.

Head. In profile subrectangular, almost glabrous, dorsal view longer than wide. Mandible with apical stepshaped teeth. Clypeus with median lobe rounded, weakly projected; median carina absent, straight in profile; lateral lobe inconspicuous. Antenna 1.14 mm; flagellar pubescence sparse; with few outstanding erect setae. First five antennal segments in ratio of about 6:3:2:2:2. Eye not gibbous, large, glabrous, located more laterally, area between anterior margin of eye and demarcation of median clypeal lobe clearly concave. Frons coriaceous-punctate. Ocelli small; posterior ocelli close to vertex crest; ocellar triangle compact; anterior ocellus not surpassing imaginary top eye line. Vertex crest convex, thick setae absent. Hypostomal carina straight.

Mesosoma. Pronotal disc as long as wide, coriaceous-punctate; anterior corner angled; posterior margin concave. Parapsidal furrow conspicuous. Mesoscutellum not reaching anterior margin of metapostnotum. Metapectal-propodeal complex with metapleural carina conspicuous.

Wings. Forewing with distal margin of 2R1 cell forming right angle; RS+M vein absent; Flexion lines not forming rectangular area, when is present only one longitudinal flexion line. Hind wing with three distal hamuli, discontinuous.

Metasoma. 2.72 × as long as wide, polished, whole surface with few setae. Ventral carina of petiole present, incomplete.

Genitalia. Sting (1vv+2vv) as long as body of genitalia; Fu wide; 1vf with apex angled; d1vf large; dorsal ramus of 2vf with superior margin of anterior region rounded, anterior margin strongly projected; 2vv as long as to 1vv; iva long, narrow; pp2vf long, narrow.

Male. Unknown.

Material examined. Holotype ♀. MADAGASCAR, Province d'Antsiranana, Ampasindava Forêt d'Ambilanivy 3.9 Km 181ºS Ambaliha, 13º47'55"S 48º9'42"E, 600 m, Malaise trap in rainforest BLF 3251, collector: Fisher, Griswold, CASENT 2114999 (CASC).

Distribution. Madagascar.

Remarks. This species is similar to *A. antemoro* **sp. nov.** by having the area between anterior margin of eye and demarcation of median clypeal lobe clearly concave, the clypeus

with median clypeal lobe rounded, the ocelli small, the vertex crest convex, and with thick setae absent, the genitalia with sting as long as the body of genitalia. However this species has the clypeus with median carina absent, the pronotal disc as long as wide, the mesoscutellum not reaching anterior margin of metapostnotum, and the forewing with flexion lines not forming a rectangular area, whereas *A. antemoro* **sp. nov.** the clypeus with median carina present, the pronotal disc shorter than wide, the mesoscutellum reaching anterior margin of metapostnotum, and the forewing with flexion lines forming a rectangular area.

***Afrobethylus antemoro* Ramos & Azevedo, sp. nov.**

(Figs 3A–D)

Description. Holotype. Female. Body length 4.6 mm; forewing 3.4 mm long. Colour. Head dark castaneous, mandible dark castaneous. Mesosoma dark castaneous. Metasoma dark castaneous.

Head. In profile subrectangular, almost glabrous, dorsal view longer than wide. Mandible with apical step shaped teeth. Clypeus with median lobe rounded, projected; median carina present, arched in profile, extending far back into frons; lateral lobe inconspicuous. Antenna 1.1 mm; flagellar pubescence sparse; with few outstanding erect setae. First five antennal segments in ratio of about 8:3:3:3:3. Eye not gibbous, large, glabrous, located more laterally, area between anterior margin of eye and demarcation of median clypeal lobe clearly concave. Frons coriaceous-punctate. Ocelli small; posterior ocelli close to vertex crest; ocellar triangle compact; anterior ocellus not surpassing imaginary top eye line. Vertex crest convex, thick setae absent. Hypostomal carina straight.

Mesosoma. Pronotal disc shorter than wide, coriaceous-punctate; anterior corner angled; posterior margin almost straight. Parapsidal furrow conspicuous. Mesoscutellum reaching anterior margin of metapostnotum. Metapectal-propodeal complex with metapleural carina conspicuous.

Wings. Forewing with distal margin of 2R1 cell forming right angle; RS+M vein absent; Flexion lines forming rectangular area, when delimited by three flexion lines. Hind wing with three distal hamuli, discontinuous.

Metasoma. 1.1 × as long as wide, polished, whole surface with few setae. Ventral carina of petiole absent.

Genitalia. Sting (1vv+2vv) as long as body of genitalia; Fu wide; 1vf with apex angled; d1vf large; dorsal ramus of 2vf with superior margin of anterior region angled, anterior margin strongly projected; 2vv as long as to 1vv; iva long, narrow; pp2vf long, narrow.

Male. Unknown.

Material examined. Holotype ♀. MADAGASCAR, Province d'Antananarivo, Botanic Garden near the entrance to Andasibe National Park, 19º55.99'S 48º24.49'E, 1026 m, 1–5 Sept[ember] 2001, Malaise trap tropical forest MA01–08B-11, collector: R. Harin'Hala, CASENT 2061590 (CASC). Paratypes. Fianarantsoa, 1 ♀, Parc National Ranomafana, radio tower at forest edge, 21º15.05'S 47º24.43'E, 1130 m, 15–21 December 2001, Malaise trap, mixed tropical forest MA-02–09B-07, collector: R. Harin'Hala CASENT 2063426 (CASC); 1 ♀, Ranomafana, JIRAMA water works, 21º14.91'S 47º27.13'E, 690 m, 21–24 December 2001, Malaise trap near river MA-02–09D-08, collector: R. Harin'Hala, CASENT 2088677 (CASC).

Distribution. Madagascar.

Variation. Body length 3.66–4.0 mm; forewing 2.83–3.0 mm long; the head with median carina of clypeus extending back into frons up to anterior margin of eye.

Remarks. This species is similar to *A. antankarana* **sp. nov.** by having the area between anterior margin of eye and demarcation of median clypeal lobe clearly concave, the clypeus with median clypeal lobe rounded, the ocelli small, the vertex crest convex, and with thick setae absent, the female genitalia with sting as long as the body of genitalia. However this species has the clypeus with median carina present, the pronotal disc shorter than wide, the mesoscutellum reaching anterior margin of metapostnotum, and the forewing with flexion lines forming a rectangular area, whereas *A. antankarana* **sp. nov.** has the clypeus with median carina absent, the pronotal disc as long as wide, the mesoscutellum not reaching anterior margin of metapostnotum, and the forewing with flexion lines not forming a rectangular area.

***Afrobethylus bapedi* Ramos & Azevedo, sp. nov.**

(Figs 4A–D)

Description. Holotype. Female. Body length 3.96 mm; forewing 2.7 mm long. Colour. Head dark castaneous, mandible dark castaneous. Mesosoma dark castaneous. Metasoma dark castaneous.

Head. In profile subrectangular, almost glabrous, dorsal view longer than wide. Mandible with apical combshaped teeth. Clypeus with median lobe angled, projected; median carina present, arched in profile, extending far back into frons; lateral lobe inconspicuous. Antenna 1.18 mm; flagellar pubescence sparse; with many outstanding erect setae. First five antennal segments in ratio of about 6:3:2:2:2. Eye not gibbous, large, glabrous, located more laterally, area between anterior margin of eye and demarcation of median clypeal lobe almost straight. Frons coriaceous-punctate. Ocelli small; posterior ocelli close to vertex crest; ocellar triangle compact; anterior ocellus not surpassing imaginary top eye line. Vertex crest convex, thick setae absent. Hypostomal carina straight.

Mesosoma. Pronotal disc shorter than wide, coriaceous-punctate; anterior corner rounded; posterior margin sinuous. Parapsidal furrow inconspicuous. Mesoscutellum extending beyond anterior margin of metapostnotum. Metapectal-propodeal complex with metapleural carina conspicuous.

Wings. Forewing with distal margin of 2R1 cell forming right angle; RS+M vein absent; Flexion lines not forming rectangular area, when is present only one longitudinal flexion line. Hind wing with three distal hamuli, adjacent.

Metasoma. 2.25 × as long as wide, polished, whole surface with few setae. Ventral carina of petiole present, incomplete.

Genitalia. Sting (1vv+2vv) as long as body of genitalia; Fu wide; 1vf with apex angled; d1vf large; dorsal ramus of 2vf with superior margin of anterior region rounded, anterior margin strongly projected; 2vv as long as to 1vv; iva long, wide; pp2vf long, narrow.

Male. Unknown.

Material examined. Holotype ♀. SOUTH AFRICA, Eastern Cape, Asante Sana Game Reserve, 34º14.990'S 24º55.962'E, 2183 m, 23 Feb[ruary]-7 April 2010, S. van Noort, Karoo Escarpment Grassland, Malaise trap ASA09-GRA1-M03, SAM-HYM A026916 (ISAM).

Distribution. South Africa.

Remarks. This species is similar to *A. antemoro* **sp. nov.** by having the head almost without setae, the vertex crest convex, and with thick setae absent, the area between anterior margin of eye and demarcation of median clypeal lobe clearly concave, and sting as long as the body of genitalia. However this species has the median clypeal carina not extending back into frons, the anterior corner of pronotal disc rounded, the mesoscutellum extending beyond anterior margin of metapostnotum, and the forewing with flexion lines not forming a rectangular area, whereas *A. antemoro* **sp. nov.** has the median clypeal carina extending back

into frons, the anterior corner of pronotal disc angled, the mesoscutellum not extending beyond anterior margin of metapostnotum, and the forewing with flexion lines forming a rectangular area.

***Afrobethylus swazi* Ramos & Azevedo, sp. nov.**

(Figs 5A–D)

Description. Holotype. Female. Body length 3.86 mm; forewing 2.59 mm long. Colour. Head dark castaneous, mandible dark castaneous. Mesosoma dark castaneous. Metasoma dark castaneous.

Head. In profile subrectangular, almost glabrous, dorsal view longer than wide. Mandible with apical combshaped teeth. Clypeus with median lobe angled, projected; median carina present, arched in profile, extending far back into frons; lateral lobe inconspicuous. Antenna 0.93 mm; flagellar pubescence sparse; with few outstanding erect setae. First five antennal segments in ratio of about 6:3:3:3:3. Eye not gibbous, large, glabrous, located more laterally, area between anterior margin of eye and demarcation of median clypeal lobe almost straight. Frons coriaceous-punctate. Ocelli small; posterior ocelli close to vertex crest; ocellar triangle compact; anterior ocellus not surpassing imaginary top eye line. Vertex crest straight, thick setae absent. Hypostomal carina straight.

Mesosoma. Pronotal disc shorter than wide, coriaceous-punctate; anterior corner rounded; posterior margin sinuous. Parapsidal furrow inconspicuous. Mesoscutellum extending beyond anterior margin of metapostnotum. Metapectal-propodeal complex with metapleural carina conspicuous.

Wings. Forewing with distal margin of 2R1 cell not forming right angle; RS+M vein absent; Flexion lines not forming rectangular area, when is present only one longitudinal flexion line. Hind wing with three distal hamuli, adjacent.

Metasoma. 1.9 × as long as wide, polished, whole surface with few setae. Ventral carina of petiole present, incomplete.

Genitalia. Sting (1vv+2vv) longer than body of genitalia; Fu wide; 1vf with apex angled; d1vf large; dorsal ramus of 2vf with superior margin of anterior region angled, anterior margin strongly projected; 2vv shorter than 1vv; iva long, wide; pp2vf long, narrow.

Male. Unknown.

Material examined. Holotype ♀. SOUTH AFRICA, Kawa*zulu*-Natal, Coleford Natural Reserve (18.6 km 212º SW Underberg), 29º57.393'S 29º27.155'E, 8–11.xii.2001, Malaise trap

UN01-SR1-M52, S. van Noort, Moist Upland Grassland on sandstone, SAM-HYM A026923 (ISAM).

Distribution. South Africa.

Remarks. This species is similar to *A. bapedi* **sp. nov.** by having the area between anterior margin of eye and demarcation of median clypeal lobe clearly concave, the vertex crest straight, and with thick setae absent, the mesoscutellum extending beyond anterior margin of metapostnotum, and the forewing with flexion lines not forming a rectangular area. However this species has the forewing with 2R1 cell not forming a right angle, and the genitalia with the sting only slightly longer than the body of genitalia, whereas *A. bapedi* **sp. nov.** has the forewing with 2R1 cell forming a right angle, and the female the sting as long as the body of genitalia.

***Afrobethylus vezo* Ramos & Azevedo, sp. nov.**

(Figs 6A–D)

Description. Holotype. Female. Body length 3.7 mm; forewing long 3.14 mm. Colour. Head dark castaneous, mandible castaneous. Mesosoma dark castaneous. Metasoma dark castaneous.

Head. In profile subtriangular, almost glabrous, dorsal view longer than wide. Mandible with apical stepshaped teeth. Clypeus with median lobe angled, projected; median carina present, arched in profile, extending far back into frons; lateral lobe inconspicuous. Antenna 1.1 mm; flagellar pubescence sparse; with many outstanding erect setae. First five antennal segments in ratio of about 6:3:2:2:2. Eye gibbous, large, glabrous, located more laterally, area between anterior margin of eye and demarcation of median clypeal lobe almost straight. Frons coriaceous-punctate. Ocelli large; posterior ocelli close to vertex crest; ocellar triangle compact; anterior ocellus not surpassing imaginary top eye line. Vertex crest straight, thick setae present. Hypostomal carina straight.

Mesosoma. Pronotal disc shorter than wide, coriaceous-punctate; anterior corner rounded; posterior margin sinuous. Parapsidal furrow inconspicuous. Mesoscutellum not reaching anterior margin of metapostnotum. Metapectal-propodeal complex with metapleural carina conspicuous.

Wings. Forewing with distal margin of 2R1 cell forming right angle; RS+M vein very short, represented by no more than angulate projection almost imperceptible arising from 1Rs

vein; Flexion lines forming rectangular area, when delimited by three flexion lines. Hind wing with three distal hamuli, discontinuous.

Metasoma. 1.75 × as long as wide, polished, whole surface with few setae. Ventral carina of petiole present, incomplete.

Genitalia. Sting (1vv+2vv) longer than body of genitalia; Fu narrow; 1vf with apex not angled; d1vf small; dorsal ramus of 2vf with superior margin of anterior region rounded, anterior margin weakly projected; 2vv shorter than 1vv; iva short, narrow; pp2vf long, narrow.

Male. Unknown.

Material examined. Holotype ♀. MADAGASCAR, Province Fianarantsoa, Parc National Ranomafana, Vohiparara at broken bridge, 21º13.57'S 47º22.19'E, 1110 m, 25 July - 3 August 2002, Malaise trap in high altitude rainforest MA-02–09A-36, collector: R. Harin'Hala, CASENT 2064074 (CASC). Paratypes. MADAGASCAR, 1♀, Province Diego-Suarez, Parc National Montagne d'Ambre, 12º30'52"S 49º10'53"E, 960 m, 4–19 Mar[ch] 2001, Malaise trap MA01–01A-08, collector: R. Harin'Hala, CASENT 2061211 (CASC); 1 ♀, Province d'Antananarivo, Botanic Garden near the entrance to Andasibe National Park, 19º55.99'S 48º24.49'E, 1026 m, 1–5 Sept[ember] 2001, Malaise trap tropical forest MA01–08B-11, collector: R. Harin'Hala, CASENT 2061934 (CASC).

Distribution. Madagascar.

Variation. Body length 3.33–3.83 mm; forewing 2.66–3.16 mm long; head with the area between anterior margin of eye and demarcation of median clypeal lobe slightly concave; the vertex crest with few thick setae.

Remarks. This species is very different of the others by having the head with ocelli large, the mesoscutellum not reaching anterior margin of metapostnotum, and the sting at least 2x longer than the body of genitalia.

Afrobethylus zulu Ramos & Azevedo, sp. nov.

(Figs 7A–D)

Description. Holotype. Female. Body length 5.14 mm; forewing 2.96 mm long. Colour. Head dark castaneous, mandible dark castaneous. Mesosoma dark castaneous. Metasoma dark castaneous.

Head. In profile subtriangular, with many setae, dorsal view longer than wide. Mandible with apical comb shaped teeth. Clypeus with median lobe angled, projected; median carina

present, arched in profile, extending far back into frons; lateral lobe conspicuous. Antenna 1.48 mm; flagellar pubescence sparse; with few outstanding erect setae. First five antennal segments in ratio of about 7:2:3:3:3. Eye not gibbous, large, with sparse pilosity, located more laterally, area between anterior margin of eye and demarcation of median clypeal lobe almost straight. Frons coriaceous-punctate. Ocelli small; posterior ocelli close to vertex crest; ocellar triangle compact; anterior ocellus not surpassing imaginary top eye line. Vertex crest straight, thick setae present. Hypostomal carina straight.

Mesosoma. Pronotal disc shorter than wide, coriaceous-punctate; anterior corner angled; posterior margin sinuous. Parapsidal furrow inconspicuous. Mesoscutellum extending beyond anterior margin of metapostnotum. Metapectal-propodeal complex with metapleural carina inconspicuous.

Wings. Forewing with distal margin of 2R1 cell forming right angle; RS+M vein very short, represented by no more than angulate projection almost imperceptible arising from 1Rs vein; Flexion lines not forming rectangular area, when is present only one longitudinal flexion line. Hind wing with four distal hamuli, discontinuous.

Metasoma. 2.13 × as long as wide, polished, whole surface with few setae. Ventral carina of petiole present, incomplete.

Genitalia. Sting (1vv+2vv) longer than body of genitalia; Fu wide; 1vf with apex angled; d1vf large; dorsal ramus of 2vf with superior margin of anterior region angled, anterior margin weakly projected; 2vv shorter than 1vv; iva long, narrow; pp2vf short, wide.

Male. Unknown.

Material examined. Holotype ♀. SOUTH AFRICA, Western Cape, Gamkaberg Nature Reserve, 33º43.745'S 21º56.972'E, 1000 m, 21 Mar[ch]-23 May 2009, S. van Noort, Renosterveld, Malaise trap GB09-REN1-M10, SAM-HYM A026913 (ISAM). Paratypes. SOUTH AFRICA, Western Cape, Gamkaberg Nature Reserve, 1 ♀, 33º43.745'S 21º56.972'E, 1000 m, 31 July-10 Sept[ember] 2009, S. van Noort, Renosterveld, Malaise trap GB09-REN1-M19, SAM-HYM A022327 (ISAM); 1 ♀, 33º43.745'S 21º56.972'E, 1000 m, 10 Sept[ember]-4 Nov[ember] 2009, S. van Noort, Renosterveld, Malaise trap GB09-REN1-M24, SAM-HYM A022328 (ISAM); 2 ♀, 33º43.745'S 21º56.972'E, 1000 m, 23 May-31 July 2009, S. van Noort, Renosterveld, Malaise trap GB09-REN1-M14, SAM-HYM A022375 (ISAM); 1 ♀, 33º39.504'S 21º53.947'E, 322 m, 19 Feb[ruary]-30 Mar[ch] 2010, S. van Noort, Gamka Thicket, Malaise trap GB09-SUC4-M32, SAM-HYM A026920 (ISAM).

Distribution. South Africa.

Variation. Body length 3.33–4.33 mm; forewing 2.33–2.66 mm long; eye with few setae; vertex crest with few thick setae.

Remarks. This species is very different of the others by having the head with eye with many setae, the genitalia with pp2vf of the 2vf short, and wide.

Discussion

Bethylinae are worldwide as a whole group. However each genus has its own pattern of distribution. Three are endemic to one zoogeographical region, *Prosierola* Kieffer, 1905 and *Lytopsenella* Kieffer, 1911 are confined to Neotropical region (Azevedo 2008, 2009, respectively), *Eupsenella* Westwood, 1874 is restricted to Australian region (Ramos & Azevedo 2012). *Sierola* Cameron, 1881 is mostly from Australian region (Fullaway 1920, 1935), only three of the 206 are non-Australian species, two are from Eastern Asia, and from U.S.A., probably introduced (Evans 1978). This can be true possibly also to single Chinese species and species from Russian Far East. Bethylus Latreille, 1802 is Holoarctic (Polaszek & Krombein 1994) and Odontepyris Kieffer, 1904 is from Old World (Polaszek & Krombein 1994). Only Goniozus Förster, 1856 is worldwide in distribution (Polaszek & Krombein 1994). The new genus *Afrobethylus* is the third one of Bethylinae recorded from Afrotropical region, and is confined to the southern area of this region (South Africa and Madagascar).

Afrotropical region is the second most species-rich zoogeographical region in the world (Cowling & Hilton-Taylor 1994). According to Sholtz and Mansell (2009) the Afrotropical region displays exceptional biological diversity because of its high numbers of biomes including deserts, forests, savannas, lake systems, the eastern mountain arc, and the tremendously rich Cape region. The Afrotropical hymenopteran fauna has been demonstrated a huge potential of new discoveries with more than 80% of the taxa described as new to science, such as Alencar and Azevedo (2011), Azevedo (2014), Azevedo and Mugrabi (2014), Barbosa and Azevedo (2012), Waichert and Azevedo (2012) for Bethylidae; Yoder et al. (2014) for Platygastridae; Rousse et al. (2013) for Ichneumonidae.

Afrobethylus **gen. nov.** is a remarkable genus of Bethylinae because its species have an unusual combination of characters which mixes features distinctive features of two genera, Bethylus and Sierola. This genus have the antenna with 10 flagellomeres, the forewing with radial cell (R) shorter than first cubital cell (1Cu), and first medial cell (1M) absent as Bethylus. On the other hand, it has the ventral carina of petiole present, and the second radial cell (2R1) closed, long, and triangular as Sierola. Moreover, it has some unique features such

as the female genitalia with dorsal ramus of second valvifer broadly enlarged (Fig. 1D), and the proximal projection starting from the base of second valvifer (Fig. 1G).

The species of *Afrobethylus* gen. nov. showed up some distinctive morphological ground plan. One of them is the setae on the eyes. Some species have their eyes completely glabrous such as *A. antankarana* **sp. nov.**, *A. antemoro* **sp. nov.**, but *A. zulu* **sp. nov.** has its eyes densely setose. This variation is also found in Bethylus (Polaszek & Krombein 1994).

An unexpected and unknown pattern for Bethylinae was observed in *A. bapedi* **sp. nov.**, *A. swazi* **sp. nov.**, and *A. zulu* **sp. nov.** whose have the mesoscutellum overlapping the anterior area of metapostnotum (Figs 4D, 5D, and 7D).

The variation of flexion lines is also conspicuous. In *A. antemoro* **sp. nov.** and *A. vezo* **sp. nov.** three flexion lines designs a rectangular area (Fig. 1B), whereas in *A. antankarana* **sp. nov.**, *A. bapedi* **sp. nov.**, *A. swazi* **sp. nov.**, and *A. zulu* **sp. nov.** have only a single longitudinal flexion line (Fig. 1C). The sting (1vv+2vv) can also vary greatly in length.

The sting of *A. antankarana* **sp. nov.**, *A. antemoro* **sp. nov.**, and *A. bapedi* **sp. nov.** is as long as the whole body of genitalia (Figs 2C, 3C, and 4C), whereas in *A. swazi* **sp. nov.**, *A. vezo* **sp. nov.**, and *A. zulu* **sp. nov.** the sting is clearly longer than the body of genitalia (Figs 5C, 6C, and 7C).

This study represents the first approach regarding on the comprehension of female genitalia of Bethylidae. We were able to identify taxonomic features on the female genitalia useful for both species and genus levels.

Traditionally the specialists on Bethylidae have been neglected the characters of female genitalia in their taxonomic studies.

This scenario is different in other Hymenoptera groups. There are several papers on hymenopteran ovipositor that show their taxonomic relevance (e.g. Snodgrass 1956, Oeser 1961, Scudder 1961, Smith 1970, Quicke et al. 1999, Vilhelmsen 2000, Vilhelmsen et al. 2001, Packer 2003). Herein, of the characters found in the female genitalia of *Afrobethylus* gen. nov. demonstrated to be decisive to establish generic boundary accurately.

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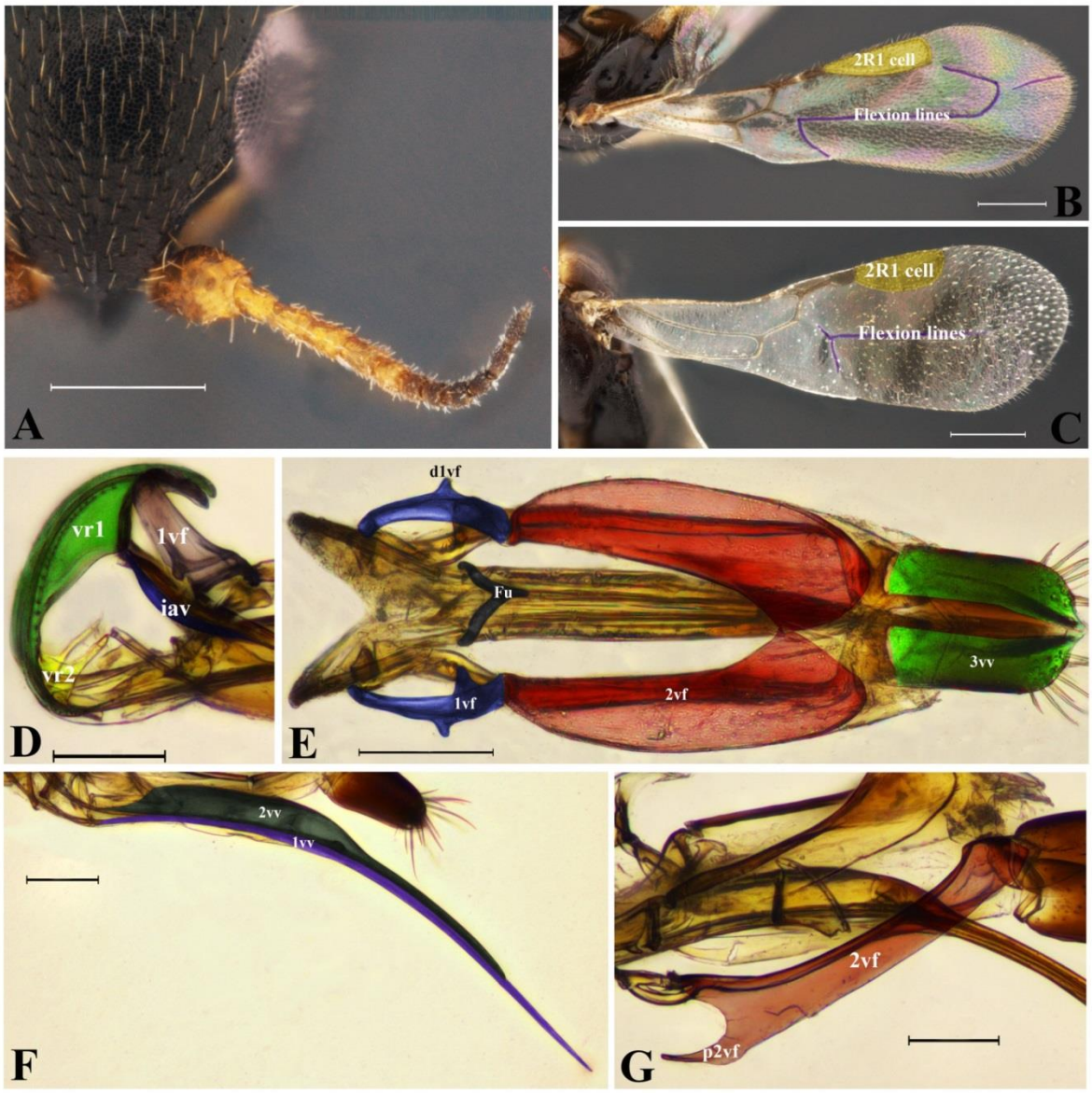

FIGURE 1. *Afrobethylus* Ramos & Azevedo **gen. nov.**. A. Antenna; B. Right forewing forming rectangular area; C. Right forewing not forming rectangular area; D–G. Main characters of female genitalia. (Scale bar: 100 µm for female genitalia; and 200 µm for antenna, and forewings.)

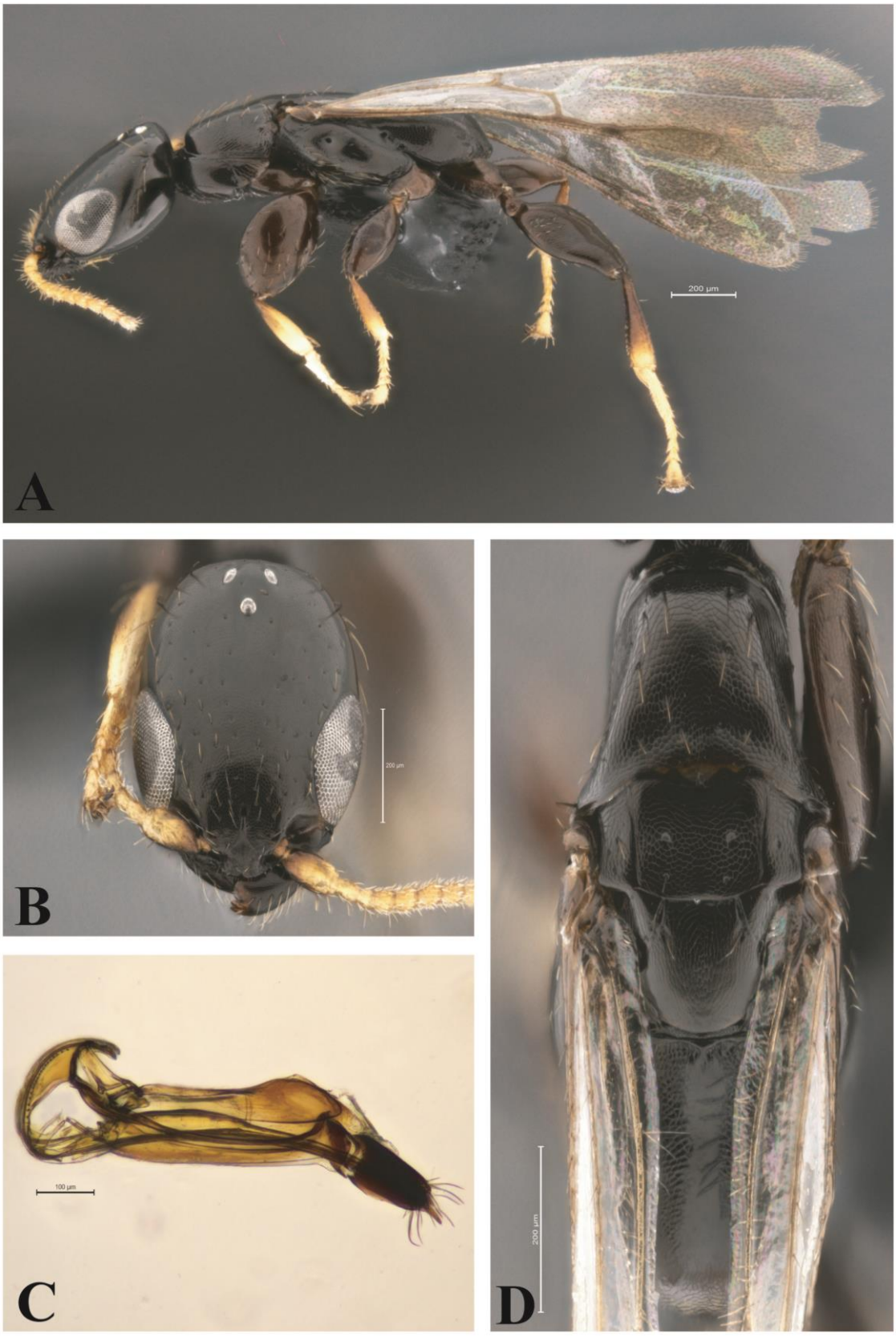

FIGURE 2. *Afrobethylus antankarana* Ramos & Azevedo **sp. nov.** holotype, ♀. A. Habitus lateral; B. Head, dorsal view; C. Genitalia, lateral view; D. Mesosoma, dorsal view.

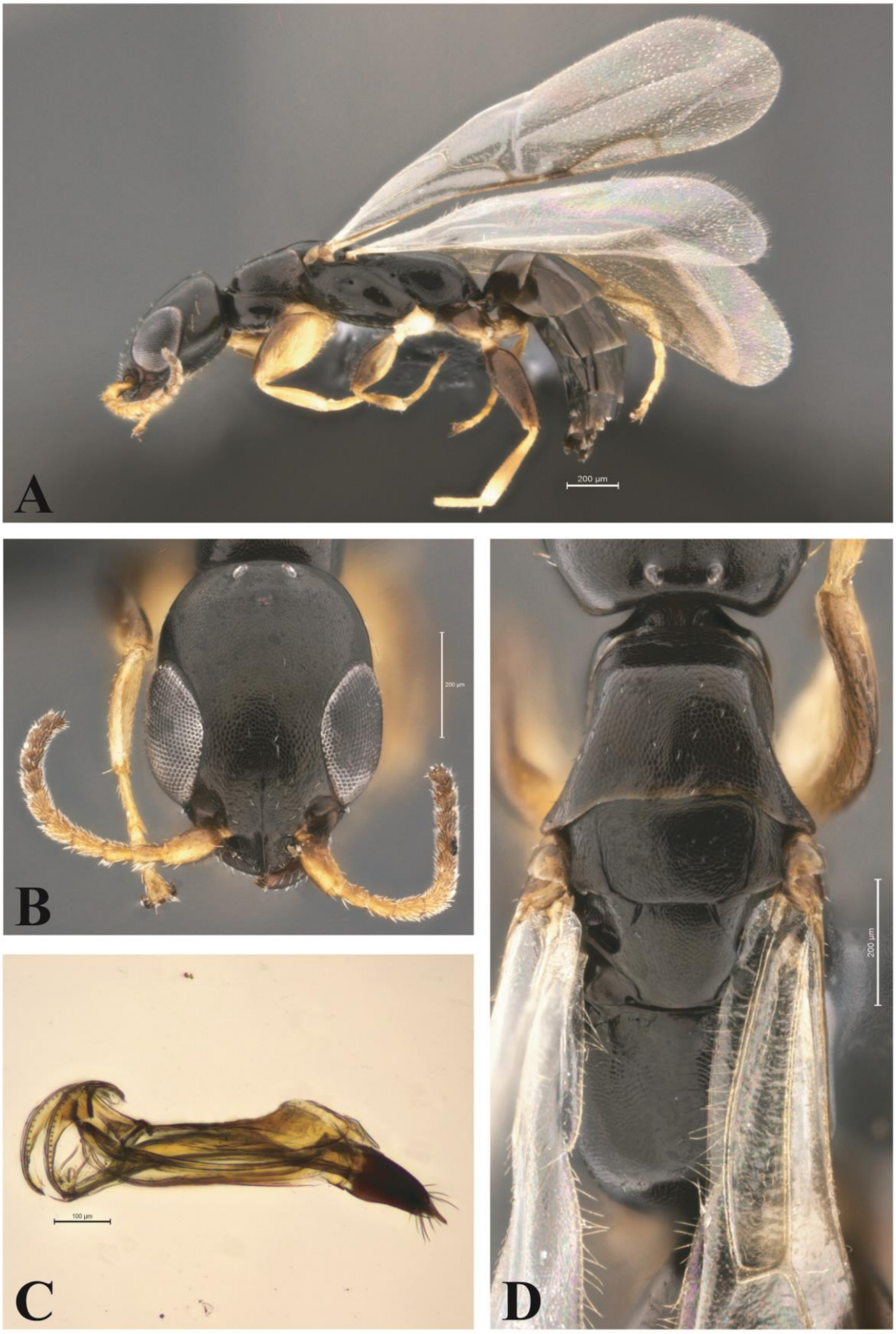

FIGURE 3. *Afrobethylus antemoro* Ramos & Azevedo **sp. nov.** holotype, ♀. A. Habitus lateral; B. Head, dorsal view; C. Genitalia, lateral view; D. Mesosoma, dorsal view.

FIGURE 4. *Afrobethylus bapedi* Ramos & Azevedo **sp. nov.** holotype, ♀. A. Habitus lateral; B. Head, dorsal view; C. Genitalia, lateral view; D. Mesosoma, dorsal view.

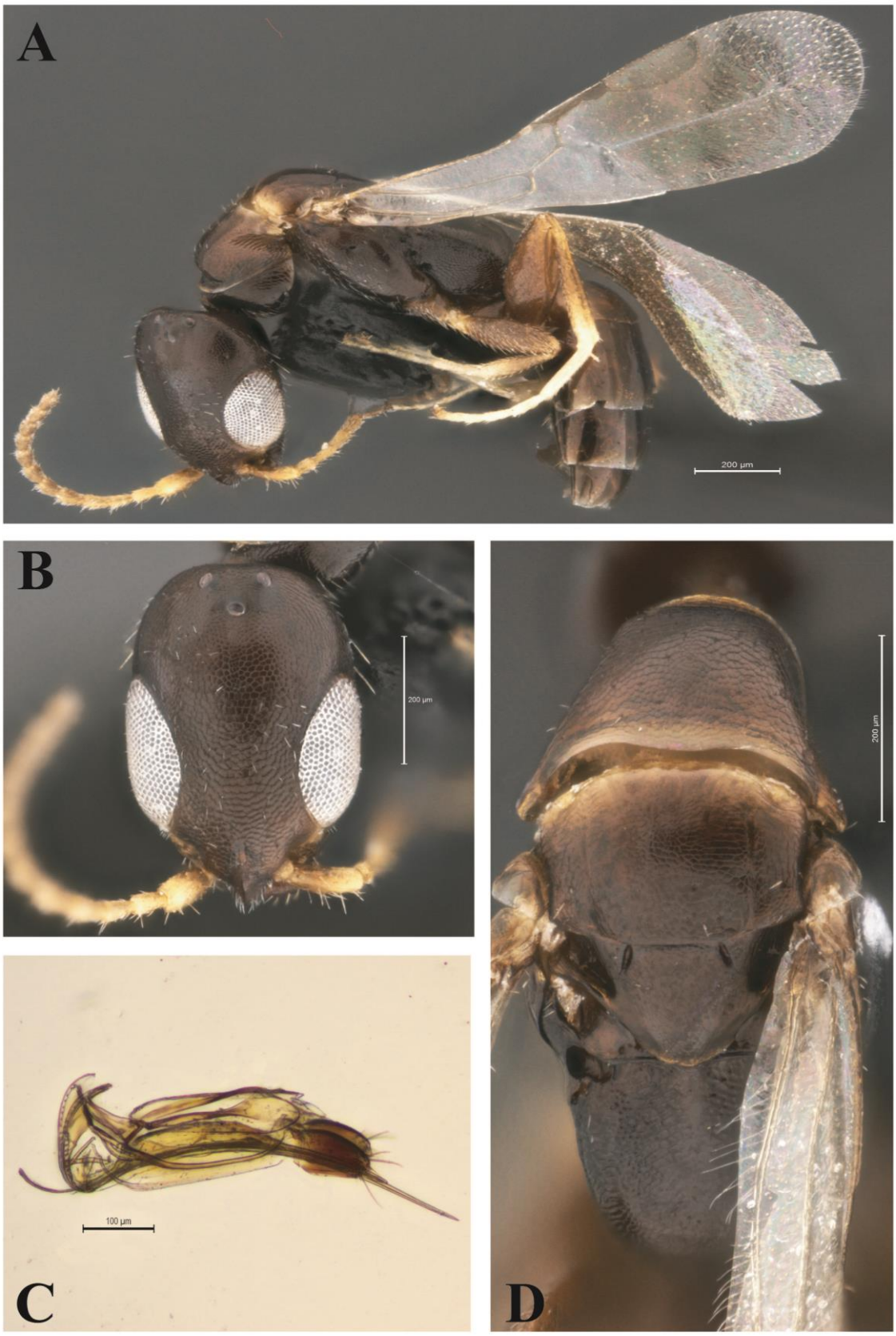

FIGURE 5. *Afrobethylus swazi* Ramos & Azevedo **sp. nov.** holotype, ♀. A. Habitus lateral; B. Head, dorsal view; C. Genitalia, lateral view; D. Mesosoma, dorsal view.

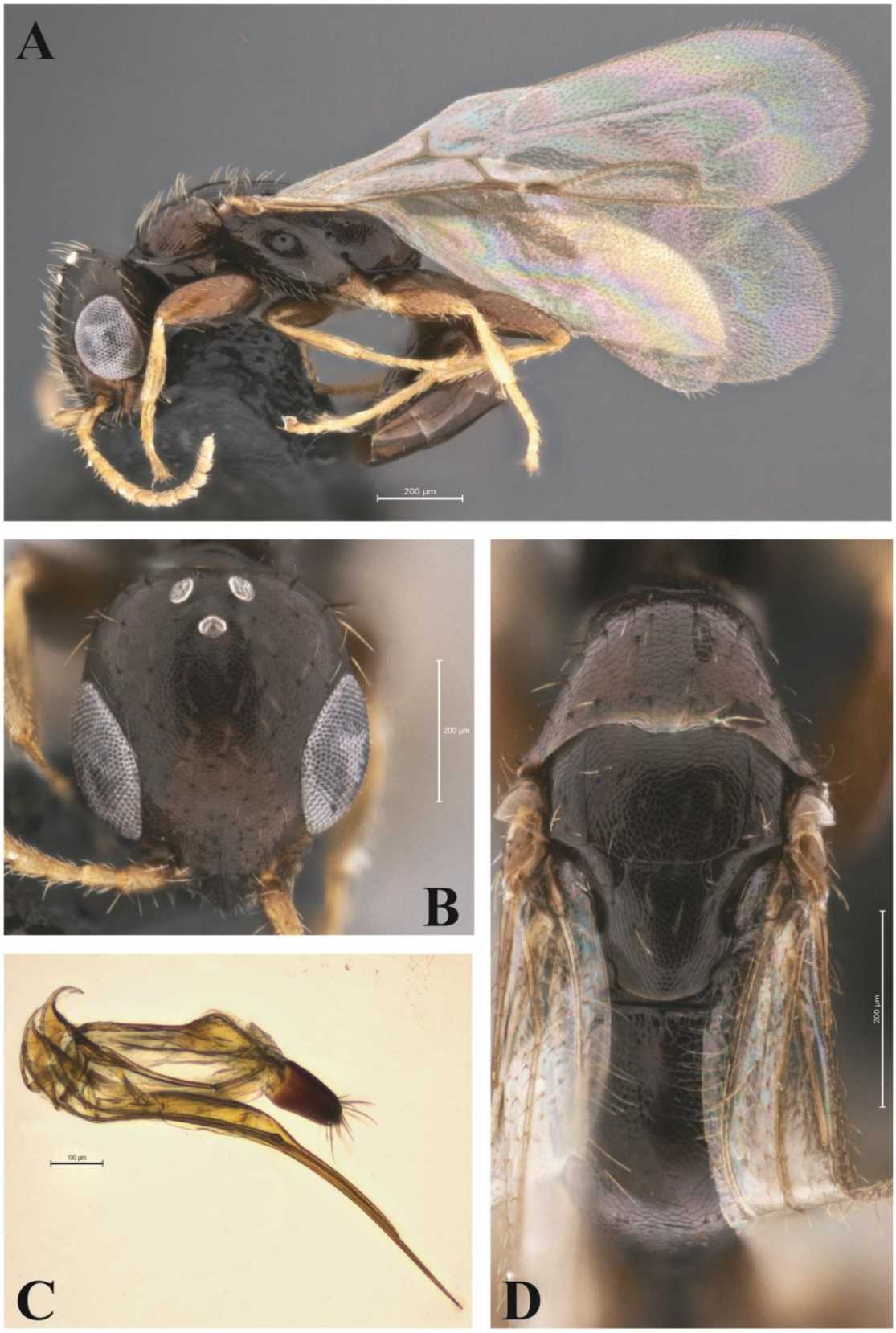

FIGURE 6. *Afrobethylus vezo* Ramos & Azevedo **sp. nov.** holotype, ♀. A. Habitus lateral; B. Head, dorsal view; C. Genitalia, lateral view; D. Mesosoma, dorsal view.

FIGURE 7. *Afrobethylus zulu* Ramos & Azevedo **sp. nov.** holotype, ♀. A. Habitus lateral; B. Head, dorsal view; C. Genitalia, lateral view; D. Mesosoma, dorsal view.

CÁPITULO 3

REVISITED PHYLOGENY OF BETHYLINAE (HYMENOPTERA, BETHYLIDAE) RESOLVES BASAL POLYTOMY

Abstract

Bethylinae are a morphologically well-defined subfamily of Bethylidae, with remarkable characters, such as clypeal carina strongly convex in lateral profile and tarsal claws bifid, strongly angled. However, there is no consensus about the cladistic relationships among their genera, mainly on *Eupsenella* and *Lytopsenella* with the other extant Bethylinae genera. To resolves this problem, a phylogeny of the Bethylinae is inferred for the first time based on a parsimony analysis of 43 and 44 morphological characters for males and females, respectively. We present a phylogenetic analysis of the subfamily, including a total 148 species in eight valid genera of Bethylinae. Moreover, male and female characters were added in these analyses by the first time. Here, we suggest practicable approaches to functional morphology, support and deformability of forewings for the first time. The data were analyzed under implied weights. Seven of the eight valid genera were retrieved as monophyletic groups. *Goniozus*, retrieved as paraphyletic group in all topologies.

Key words Insecta, Chrysidoidea, Systematics, genitalia, deformability, forewing.

Introduction

Bethylinae currently comprise approximately 540 nominal species worldwide classified in eight extant genera. The hypothesis that Bethylinae are monophyletic was proposed by Carpenter (1999). They display a fascinating diversity in their behavior and exceptional uniformity in their host preferences, main related to Lepidoptera species larvae.

The genera of this subfamily, at least apparently, are clearly different one from another, and their taxonomic boundaries are well established, except for *Goniozus* Förster. However, considering the phylogenetic scenario, hitherto, there are not accurate and consistent analyses for explaining theie internal phylogenetic sister-group relationships.

The phylogeny of Bethylinae has received attention by Sorg (1988), Polaszek & Krombein (1994), Terayama (1995) and De Ploëg & Nel (2004). Nonetheless, the relationships of this subfamily remain mostly uncertain and some doubts about relationship among their genera. In all previous analyses performed there is a basal polytomy among *Eupsenella* Westwood, *Lytopsenella* Kieffer and the remaining Bethylinae genera. Probably, this scenario can be related to the fact that these analyses were performed, based on a reduced number of ingroup

taxa and reduced zoogeographic sampling, which may have resulted in a undersampling of possible morphological diversity attributed to each genus.

The wing venation of Bethylinae is a valuable taxonomic tool because there is specific and well-established pattern for each genus. However, its phylogenetic potentialities are distant of be fully exploited in this subfamily. The important peculiarity about the forewing in Bethylinae is that the veins which bound and form the forewing cells have received little attention. The reason for this approach probably can be found in the inconsistencies and difficulties of homologizing the wing veins of the entire Bethylinae groups. Moreover, many other aspects of forewing venational features, such as flexion lines, areas specialized for deformability, for support, and some possible structural adaptations for these roles also have received little attention.

Given this scenario, the aims of the present study are: (1) to propose a phylogenetic hypothesis of the genera of Bethylinae drawing especial attention to *Eupsenella* and *Lytopsenella* relationships with the other genera of this subfamily, (2) to outline the arrangement of veins, deformable areas and flexion lines under functional morphology approach, and (3) to investigate and discuss the evolution of the main diagnostic characters of Bethylinae genera.

Material and methods

Taxon sampling

The material used in this study is deposited in the following research institutions: **ANIC**, Australian National Insect Collection, Australia (N. Fisher); **BMNH**, The Natural History Museum, London, UK (D. Notton); **BPBM**, Bernice P. Bishop Museum, USA (J. Boone); **CASC**, California Academy of Sciences, USA (R. Zuparko); **NZAC**, New Zealand Arthropod Collection, New Zealand (D. Ward); **ISAM**, Iziko South Africa Museum, South Africa (S. van Noort); **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (A.R. Alsina); **MNHN**, Muséum National d'Histoire Naturelle, France (C. Villemant); **UFES**, Universidade Federal do Espírito Santo, Brazil (M.T. Tavares); **USNM**, National Museum of Natural History, USA (B. Harris).

Morphological character limitation

Character limitation was conducted following Rieppel & Kearney (2002). The characters analyzed here were treated as hypotheses of homology following Nixon & Carpenter (2012). External morphology was studied through examination of dry, pinned specimens. Both adult males and females when available were examined separately for character limitation. The genital capsules were detached from the metasoma and Proteinase K was used for digestion of muscles, and then displaying only the sclerites. The anatomical data treated here are consistent with the Hymenoptera Anatomy Ontology project (HAO) (Yoder et al. 2010; Seltmann et al. 2012). The terminology used by female genitalia follows the HAO project, and Ramos & Azevedo (2016). The wing venation nomenclature used in this paper follows Ramos & Azevedo (2012). The terms applied to the structures follow Kawada et al. (2015).

Morphological data

The morphological data were mainly taken from earlier studies (Polaszek & Krombein 1994; Terayama 1995; De Ploëg & Nel 2004). De Ploëg & Nel (2004) proposed their analyses based only on the combination and reinterpretation of the characters proposed by Polaszek & Krombein (1994) and Terayama (1995). In this paper, we revised the morphological data set of De Ploëg & Nel (2004), and expanded it to include all valid genera of Bethylinae, as for instance *Afrobethylus* Ramos & Azevedo recently described by Ramos & Azevedo (2016). Moreover, some characters were excluded or reinterpreted because they cannot be satisfactorily examined in Bethylinae species. We also added new characters that were well suited to examination in Bethylinae species, such as the characters of male and female genitalia. The pattern of distribution of character states was based on strict consensus tree.

Outgroup selection

The outgroup are composed of four Chrysidoidea species from Chrysididae, Plumariidae, Sclerogibbidae, and Scolebythidae (Tables 1, 2 and 3). The outgroup taxa were selected based on their phylogenetic proximity to Bethylinae (Carpenter 1999). According to Carpenter (1999) Plumariidae are the sister-group of all families, therefore we decided to select this family as outgroup and root to our analysis.

Ingroup selection

The species analyzed represent all living genera described to Bethylinae (Tables 1, 2 and 3) and cover all zoogeographical regions sense Wallace (1876) where the genera have records. The species were selected to cover the maximum possible morphological diversity attributed to each genus to facilitate possible taxonomic decisions.

The resulting matrices contain a total of 61 species of Bethylinae terminals as ingroup, with a total of 43 adult characters coded for males and a total of 87 species, with a total of 44 adult characters were coded for females. These Bethylinae terminals selected cover all living genera, namely: only females for *Afrobethylus* (males unknown), males and females for *Bethylus* Latreille, *Eupsenella*, *Goniozus*, *Lytopsenella*, *Odontepyris* Kieffer, *Prosierola* Kieffer and *Sierola* Cameron.

Matrix and character list

In order to construct a robust hypothesis of the relationships among the Bethylinae genera we analyzed adult males and females separately to evaluate the possible synapomorphies of the data. The character list was made in the DELTA program editor (Dallwitz 1980) and converted into the character matrices for cladistic analysis (hendata format). The character matrix was constructed in Winclada ver. 1.00.08 (Nixon 1999-2002). Most characters were treated as binary. All characters were treated as unordered. Inapplicable and unknown characters were coded with '?'.

Cladistic analyses

The searches for the most parsimonious trees were carried out under the software TNT ver. 1.1 (Goloboff et al. 2008b), using the New Technology algorithms. Parameters were as follows: collapsing rules selected for TBR; random seed was 1; Sectorial Search (Goloboff 1999) in default mode; 3000 iterations of Ratchet (Nixon 1999); Drift in default mode (Goloboff 1999); and Tree Fusing (Goloboff 1999) in default mode. The matrices data were submitted to "Traditional Search" algorithm for the search of the "Wagner trees". This protocol is to determine the parameters related to the "random seed" and the number of analysis of replication.

In this paper, we used the TNT script setk.run, written by Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucuman, Argentina), to calculate the appropriate value of K. The most appropriate value of K was chosen for each partition independently. The script returned a

value of k = 8.906250 for our data set based on males, and k = 13.349610 when based on females, which were then employed.

Branch support was investigated using symmetric resampling (Goloboff *et al.*, 2003). The Symmetric Resampling analyses were run in TNT with the traditional search (default parameters) and 100 replications. Clade support was estimated using 100 pseudoreplicates of symmetric resampling (Goloboff et al. 2003) in TNT, reported as frequency differences (GC scores) (Figs 1A, 1B).

The analyses of trees, mapping of characters and graphic manipulation were performed in Winclada 1:00:08 program (Nixon 2002).

Based on our data, in some cases, *Goniozus* was highlighted with quotation marks ("*Goniozus*") to represent it as a paraphyletic group.

Illustrations

The specimens were photographed under a Leica Z16APO stereomicroscope with a magnifying glass coupled to a Leica DFC 295 video camera by Leica Microsystems. The illustration of male and female genitalia was obtained using Leica MD2500 Microscope magnifying glass attached to a Leica DFC 495 video camera captured using Leica LAS (Leica Application Suite V3.6.0). The equipment used for data storage was a high-performance notebook with Windows 7 Professional. The software program used to combine the images was the Helicon Focus (©HeliconSoft), which uses the parameters C method, 100% full resolution and 600 DPI. The illumination of all specimens was performed according to Kawada et al. (2016). For more efficient light diffusion, a dome was used along with a tracing paper ring, which was placed around the specimens to allow for size modulation. All illustrations and plates were edited in a software for edition of images and vectorization using the adjustments (e.g., levels, shadows/highlights), tools (e.g., healing brush, clone stamp) and filters (e.g., unsharp mask), respectively. The highlights used for the characters, including arrows and different vector colors, were edited in software for edition of images and vectorization.

Results

The analyses under implied weights returned seven equally parsimonious cladograms for males (Figs 2, 3) and three for females (Figs 4, 5).

The analyses based on males retrieved a cladogram with L= 162, best score (Fit) = 4.06739, the consistency index (CI) = 0.33, and the retention index (RI) = 0.75 and concavity value K = 8.906250 (Figs 2, 3). For females we retrieved a cladogram with L= 110, best score (Fit) = 3.06450, the consistency index (CI) = 0.45, and the retention index (RI) = 0.90, and concavity value K = 13.349610 (Figs 4, 5).

The resampling analyses based on both males and females returned support for a sister-group relationship among all extant Bethylinae genera (Figs 1A-B). All genera were retrieved as monophyletic lineages in both analyses, except *Goniozus* that was retrieved as paraphyletic in relationship to *Sierola* and *Bethylus* in all analyses performed (Figs 3, 4).

One of the main results obtained is this study was that sister-group relationships among the main lineages within the Bethylinae clade showed a high level of resolution and support intergeneric relationships among the genera both in male and female analyses (Figs 1A-B).

Bethylinae were retrieved as monophyletic group and are supported by following seven synapomorphies: tarsal claws bifid (char. 23.1) (Fig. 7E), tarsal claws strongly curved (char. 24.1) (Fig. 7F), petiolar ventral carina present (char. 25.1) (Fig. 7G), female genitalia with furcula V-shaped (char. 39.1) (Fig. 8N), female genitalia with proximal projection of 2vf (char. 40.1) (Figs 8O), male hypopygium with posterior margin medially bilobed, convex and concave (char. 43.2,3,4) (Figs 8K, 8L, 8N), male hypopygium rectangular (char. 41.1) (Fig. 8J).

Our most remarkable result obtained was the resolution of the existing basal polytomy in Bethylinae between *Lytopsenella* and *Eupsenella* with the other extant Bethylinae genera (Figs 2, 4). In all analyses performed, these genera were retrieved by the first time as sister-group each other and separated from the other genera in all analyses performed.

The clade (*Lytopsenella* + *Eupsenella*) (Figs 2, 4) is supported by six synapomorphies: metapostnotum with median metapostnotal carina (char. 17.1) (Fig. 6P), spine of metacoxae with a large blunt spine (char. 22.1) (Fig. 7D), 1R1 vein ill-developed (char. 29.1) (Fig. 7M), shape of second radial cell lanceolate (char. 37.1) (Fig. 8E), male genitalia with two parameres (char. 39.1) (Fig. 8F), and male hypopygium triangular (char. 41.0) (Fig. 8I).

The monophyly of *Lytopsenella* (Figs 2B, 4B) is supported by two synapomorphies: female genitalia with basal region of 2rv broadly enlarged (char. 41.1) (Fig. 8P), and female genitalia with distal region of the dorsal area of Tergite 9 (T9) enlarged (char. 44.1) (Fig. 8S).

The monophyly of *Eupsenella* (Figs 2C, 4C) is supported by seven synapomorphies: head with eye hairy (char. 1.1) (Fig. 6A), metapectal-propodeal complex with metapostnotal-

propodeal suture conspicuous (char. 18.1) (Fig. 6Q), forewing with length of second radial cell short (char. 36.1) (Fig. 8D), forewing with shape of second radial cell elliptical (char. 37.0) (Fig. 8D), forewing with length of first radial cell longer than second radial cell (char. 38.1) (Fig. 8D), male hypopygium with posterior margin bidentate (char. 43.0) (Fig. 8I), and female genitalia with proximal margin of 1vf angled (char. 43.1) (Fig. 8R).

The clade ((*Prosierola* + *Odontepyris*) + ((*Sierola* + *Bethylus*) + *"Goniozus"*))) (Figs 2, 3) is restricted to males. This clade is supported by tree synapomorphies: mesoscutum without notaulus (char. 10.1) (Fig. 6G), forewing without first radial cell (char. 32.1) (Fig. 7Q) and forewing with second radial cell open (char. 33.1) (Fig. 7T).

The clade ((*Prosierola* + *Odontepyris*) + ((*Sierola* + (*Afrobethylus* + *Bethylus*) + *"Goniozus"*))) (Figs 3, 4) is restricted to females. This restriction is because *Afrobethylus* is known only from females. This clade is supported by tree synapomorphies: five maxillary palp articles (char. 7.1) (see more details in Polaszek & Krombein (1994), character 3, pg. 93, and in De Ploëg 2004, character 3, pg. 80), forewing without first radial cell (char. 32.1) (Fig. 7Q) and forewing with first medial cell triangular (char. 35.0) (Fig. 8B).

The clade (*Prosierola* + *Odontepyris*) (Figs 2, 4) is supported by nine synapomorphy: mesopleuron, gibbous in dorsal view (char. 11.1) (Fig. 6I), mesoscutellum with mesoscutellar groove or pits present as sulcus (char. 13.1) (Fig. 6K), mesoscutellum with mesoscutellar fovea enlarged (char. 14.1) (Fig. 6L), metapectal-propodeal complex with metapostnotal-propodeal suture conspicuous (char. 18.1) (Fig. 6Q), propodeum with posterior transverse carina of propodeal disc (char. 19.0) (Fig. 7A), forewing with 1Rs vein longer than M vein (char. 30.1) (Fig. 7N) and forewing with RS+M vein shorter than 1Rs vein (char. 34.1) (Fig. 8A).

The monophyly of *Prosierola* (Figs 2D, 4D) is supported by five synapomorphies: pronotum with posterior margin slightly produced backward medially (char. 8.1) (Fig. 6E), metapostnotum with triangular area marked dorsal smooth present (char. 15.1) (Fig. 6M), propodeum with pair of conspicuous anterior pits on the propodeal disc (char. 21.1) (Fig. 7C), male genitalia with two parameres (char. 39.1) (Fig. 8F), and female genitalia with distal region of the dorsal area of tergite 9 enlarged (char. 1) (Fig. 8S).

The monophyly of *Odontepyris* (Figs 2E, 4E) is supported by eight synapomorphies: malar space visible in profile (char. 3.0) (Fig. 6C), prosternum smaller than area of forecoxa (char. 9.0) (Fig. 6F), mesopleuron with dentate process of mesopleuron in dorsal view (char. 12.1) (Fig. 6J), metapostnotum with median metapostnotal carina present (char. 17.1) (Fig. 6P),

propodeum with a pair of pits in basal outer portion of propodeum (char. 20.1) (Fig. 7B), forewing without bula (char. 27.0) (Fig. 7J), forewing with first medial cell rectangular (char. 35.2) (Fig. 8C), and female genitalia with proximal margin of 1vf angled (char. 43.1) (Fig. 8R).

The clade ((*Sierola* + *Bethylus*) + *"Goniozus"*) (Fig. 3) is supported by one synapomorphy: head without an unsculptured streak frontally (char. 2.1) (Fig. 6B). However, this clade for males was retrieved only from of four "*Goniozus*" species (*G. angulatus, G. antileanus, G. castaneicolor* and *G. complanatus*) and supported by one synapomorphy: male hypopygium with posterior margin straight (char. 43.1) (Fig. 8J).

The clade (*Sierola* + *Bethylus*) (Fig. 3) is restricted to males. This clade is supported by four synapomorphies: two labial palp articles (char. 6.1) (see more details in Polaszek & Krombein (1994), character 2, pg. 93), forewing with angle of distal margin of Rs sector vein with a sharp angle (char. 31.1) (Fig. 7P), male genitalia without ventral projection of apical lobe of aedeagus (char. 40.0) (Fig. 8G), and male hypopygium triangular (char. 41.0) (Fig. 8I).

In this paper, we show that *Goniozus* is paraphyletic by the first time. However, *Goniozus* as a paraphyletic group contrary the results obtained by Sorg (1988), Polaszek & Krombein (1994) and De Ploëg & Nel (2004) when this genus was retrieved as a monophyletic group.

The clade (*Sierola* + (*Afrobethylus* + *Bethylus*)) (Fig. 5) is supported by three synapomorphies: two labial palp articles (char. 6.1) (see more details in Polaszek & Krombein (1994), character 2, pg. 93 , forewing with angle of distal margin of radial sector vein (Rs) in a sharp angle (char. 31.1) (Fig. 8P), and female genitalia with proximal margin of 1vf angled (char. 43.1) (Fig. 8R).

The clade (*Afrobethylus* + *Bethylus*) (Fig. 5) is supported by three synapomorphies: antenna with 10 flagellomeres equal (char. 4.2) (Fig. 6D), forewing with radial one vein (R1) ill developed (char. 29.1) (Fig. 7M), and forewing with length of radial sector + median vein (RS+M) shorter than 1Rs vein (char. 34.1) (Fig. 8A).

The monophyly of *Afrobethylus* (Fig. 5G) is supported by two synapomorphies: female genitalia, proximal projection starting from the base of 2vf broadly enlarged (char. 42.1) (Fig. 8Q), and female genitalia, basal region of 2rv broadly enlarged (char. 41.1) (Fig. 8P).

The monophyly of *Bethylus* (Figs 3F, 5H) is supported by six synapomorphies: antenna, number of flagellomeres equal to 10 (char. 4.2) (Fig. 6D), and male hypopygium, shape of posterior margin totally concave (char. 43.5) (Fig. 8M), petiolar ventral carina absent (char.

25.0) (Fig. 7H), forewing, 1R1 vein ill-developed (char. 29.1) (Fig. 7M), forewing, length of RS+M vein shorter than 1Rs vein (char. 34.1) (Fig. 8A), and male genitalia with two parameres (char. 39.1) (Fig. 8F).

The monophyly of *Sierola* (Figs 3G, 5I) is supported by three synapomorphies: four maxillary palp articles (char. 7.0) (see more details in Polaszek & Krombein (1994), character 3, pg. 93, and in De Ploëg 2004, character 3, pg. 80), 2Cu vein present (char. 28.1) (Fig. 7L), and forewing, second radial cell closed (char. 33.0) (Fig. 7S).

Discussion

According to Weins (2004) we live in the age of comparative genomics, and it may seem that there is not much point in reconstructing phylogenies using morphological data anymore.

We performed only analyses based on morphological data. We conducted our analysis based on this source by understanding that morphology still play a crucial role in alpha-taxonomy, and hence, in the phylogeny reconstruction (see more details in Scotland et al. 2003). In almost, all groups of organisms, species are described and identified based on morphological data. Morphological data are responsible for what we know about much of the phylogeny of life. In other words, most of our current knowledge of phylogeny still stems from classifications (Platnick 1979), which are in turn based on morphology.

Other issue was mentioned by Hillis & Wiens (2000), who said that dense taxon sampling is the greatest advantage of morphological data demonstrating the importance of taxon sampling for accurate phylogeny estimates (Hillis 1996, 1998; Graybeal 1998).

We observed such condition here based on our results, mainly when we compare them to the previous studies on phylogenetic relationships for Bethylinae such as Sorg (1988), Polaszek & Krombein (1994), Terayama (1995) and De Ploëg & Nel (2004).

Hitherto, in all previous analyses performed there is a basal polytomy among *Eupsenella*, *Lytopsenella* and the remaining Bethylinae genera unresolved (Fig. 9A-D). And it is not surprising, because these previous analyses were performed, based on a reduced number of taxa in the ingroup and also with reduced zoogeographic sampling, that is, not covering the possible zoogeographical regions where each Bethylinae species occurs. These results in a limited coverage of the possible morphological diversity attributed to each genus.

Based on this scenario, in this paper we perform our analyses prioritizing the quality of the data and taxa sampling as primary importance. Graybeal (1998) demonstrated that under some conditions phylogenetic accuracy was improved as the number of taxa increased, but not

when more characters were added. Thus, we scored 148 terminals (61 male species and 87 female species) instead of 13 used the previous studied aforementioned (Tables 1, 2, and 3). Moreover, we covered the main zoogeographical regions where the Bethylinae species occurs, and the main possible morphological diversity attributed to each genus. Hence, in all topologies for males and females retrieved here the basal polytomy among *Eupsenella*, *Lytopsenella* and the remaining Bethylinae genera was solved.

Topology

The topologies supported here endorse the most results found by De Ploëg & Nel (2004), except by *Goniozus* that was retrieved as paraphyletic (Fig. 9D). Among these similar results, it is worth mentioning the monophyly of the *Odontepyris* and *Prosierola*, and *Bethylus* and *Sierola*, both groups recovered as sister-groups. However, *Goniozus* was retrieved as paraphyletic group in all analyses here performed both based on male and female trees, thus counteracting the idea of monophyly proposed by Polaszek & Krombein (1994) and De Ploëg & Nel (2004).

The monophyly of *Goniozus* retrieved by Polaszek & Krombein (1994) is supported by a single synapomorphy, the "reduction of the ventral carina of petiole". Moreover, the presence of a smooth triangular area on the metapostnotum is a shared among *Goniozus* and *Prosierola* as a homoplasy. De Ploëg & Nel (2004) proposed that the clade (*"Goniozus"* + (*Sierola* + *Bethylus*)) is supported by the character "presence of an unsculptured streak frontally absent (no unsculptured streak frontally)" (char. 4.1, pg. 80).

Goniozus was retrieved as paraphyletic group cannot be regarded as a surprise for Bethylinae. Previous analyses were based only on a reduced number species of *Goniozus*. Three species to cover the several possibilities of morphological patterns of a genus with more than 170 species is not enough. However, this genus is clearly worldwide in distribution, and is the second genus in number of species in Bethylinae. Hence, establishing patterns of morphological characters for this genus is a complex task, and certainly for *Goniozus* it cannot be done accurately using only three species. Currently, such genus has two junior synonymous proposed by Evans (1978), *Parasierola* Cameron and *Perisierola* Kieffer, and present a total of 174 described species. Given the wide geographical distribution, the large number of species, the high characteristics divergence among species, is likely that genus could represent more than one lineage. But, based on our data it was not possible to retrieve clearly which are these lineages for *Goniozus*. Thus, we need further deep both

taxonomic and phylogenetic revision exclusively to investigate the morphological boundaries of *Goniozus*.

Ancestral state character reconstruction

Antenna

The number of flagellomeres is an important character from a phylogenetic perspective within Bethylinae (Sorg 1988; Polaszek & Krombein 1994; Terayama 1995; De Ploëg & Nel 2004). This number varies in several taxa at generic level. The antennae 10-flagellomered is a relevant phylogenetic signal which addresses to the monophyly of *Bethylus* on male analyses (Figs 3H, 10A), and to monophyly of the clade (*Afrobethylus* + *Bethylus*) (Figs 5G-H, 10B) on female analyses as well. Thus antennae 11-flagellomered is a plesiomorphic condition within Bethylinae. We cannot recognize if this reduction is due to lost or fusion of flagellomeres under cladistic techniques, but future histological studies may clarify that more accurately.

Forewing

Hennig (1981) stated "*The evolution of wings was the central adaptation allowing insects to escape predators, exploit scattered resources, and disperse into new niches, resulting in radiations into vast numbers of species*". Based on this scenario, Grimaldi & Engel (2005) mentioned among other things that the wings play a crucial role in understanding insect evolution. Hence, wing venation is one of the main characters used to identify and to classify insects (Comstock & Needham 1899). That is particularly true for the genera of Bethylinae, it is relatively easy to recognize the genera only through of the characters of the forewing.

The angle of the radial vein (Rs) is independent whether the 2R1 cell is closed or open. This character was retrieved as a synapomorphies for the clade (*Bethylus* + *Sierola*) (Figs 3, 11A), and for the clade ((*Afrobethylus* + *Bethylus*) + *Sierola*) (Figs 5, 11B). It is worth mentioning that De Ploëg & Nel (2004) considered it as ambiguous because the radial vein has a strong curve in *Eupsenella*, and such condition would be rather similar to those of *Sierola* and *Bethylus*, with a strong distal angle. However, we considered a sharp angle when the radial vein form an angle of 90° to a given surface, in this case with the anterior margin of the forewing. Therefore, this condition is present only *Afrobethylus*, *Bethylus* and *Sierola*

(Fig. 11A-B) effectively had shown Rs vein with a sharp angle. Thus, it was retrieved as synapomorphy for these three genera.

Another pattern in the forewing is related to second radial cell (2R1) closed when the Rs vein reaches the anterior margin of the forewing. For Bethylinae, 2R1 cell, called by the former authors of marginal cell, is present and closed in *Afrobethylus*, *Eupsenella*, *Lytopsenella*, and *Sierola*. The 2R1 cell closed is ambiguous, because it has at least two independent origins in males (Fig. 12A), and five for females (Fig. 12B). Thus, it does not represent a clear phylogenetic signal for any genera in Bethylinae.

In Bethylinae, the first radial cell (1R1), called by the former authors of submarginal cell, is present and closed only in *Eupsenella* and *Lytopsenella* (Fig. 13A-B). This character is absent in all remaining genera of Bethylinae. The absence of 1R1 cell is found in ((*Prosierola* + *Odontepyris*) + ((*Sierola* + *Bethylus*) + *"Goniozus"*))) (Figs 2, 3), and in ((*Prosierola* + *Odontepyris*) + ((*Sierola* + (*Afrobethylus* + *Bethylus*) + *"Goniozus"*))) (Figs 4, 5) and represent a synapomorphy to these assemblages.

One of the main patterns observed for the forewing in Bethylinae genera is shown in *Lytopsenella*, *Eupsenella*, *Prosierola*, and *Sierola*, whose the first medial cell (1M) is always closed when RS+M, and 2Cu veins are present and complete (traditionally called areolet) and in the species of *Afrobethylus* and *Bethylus*, whose the 1M cell is always opened, when at least 2Cu vein is absent. However, there also are two genera with the both patterns, *Goniozus* and *Odontepyris*. These genera have species with first medial cell both closed and opened. The presence of 2Cu vein (Fig. 7L) for all Bethylinae genera was retrieved as ambiguous (Fig. 14A-B). There were for such character at least 15 independent origins in the male tree, and 10 in the female tree. Moreover, the length of RS+M vein (Fig. 8A) was also retrieved as ambiguous. There were for such character at least eight independent origins in the male tree, and six in the female tree (Fig. 15A-B). Thus, this character also does not represent phylogenetic signal for any genera in Bethylinae. The variation in wing venation is one of the most characteristic features of insect species.

Many wing venation characters in Bethylinae are homoplastic, especially the presence versus absence of the first medial cell. The forewing of Bethylinae displays a wide range of variation of their cells and veins. However they are very useful for alpha taxonomic generic delimitation.

The C, R and 1Cu cells are always closed in all genera of Bethylinae. The clade (*Lytopsenella* + *Eupsenella*) (Figs 2, 4) is marked by having species always with six closed

cells in the forewing. However, in *Lytopsenella* the 1R1 cell of the forewing always significantly shorter than the 2R1 cell, whereas in *Eupsenella* this cell is at most as long as the 2R1 cell. Both genera have some fossil species, they are much alike to the extant species (Ramos & Azevedo 2012). These patterns are very similar to the fossil subfamily Lancepyrinae. This Lebanese fossil has a mosaic of plesiomorphic and apomorphic features used to define subfamilies within Bethylidae Azevedo & Azar (2012).

Another clade retrieved was ((*Prosierola* + *Odontepyris*) + ((*Sierola* + *Bethylus*) + *"Goniozus"*))) for males (Figs 2, 3), and the clade ((*Prosierola* + *Odontepyris*) + ((*Sierola* + (*Afrobethylus* + *Bethylus*) + *"Goniozus"*))) for females (Figs 4, 5). The species found in this clade are characterized by having the forewing with three, four or five closed cells. This condition is found when the first medial, first radial and second radial cells in *Goniozus* (*sensu strictu*), *Bethylus* and *Odontepyris* (only three closed cells) are opened. Moreover, there is one more pattern in Bethylinae that is with four closed cells, but with a different combination of these. There is another pattern in *Afrobethylus*, whose the first medial cell is absent, but the second radial cell is present and closed, so that its forewings have four closed cells, but with a different arrangement. Finally, *Sierola* is the genus with most closed cells in this clade, because the only cell opened is the first radial cell.

Given these data, we postulate that the ground plan of bethylines is the forewing with six closed cells with trend of reduction of this number by distinct arrangements resulted by different loss of cells. However, the number of closed cells found in these genera is probably related to the particular adaptation process of these lineages to the environment. We suggest that probably the deep homology as an important process for the generation these novelties in the bethylines forewing. About such scenario Shubin et al. (2009) mentioned that the similarities are much more than the use of a common genetic tool kit of genes. Thus, such similarities probably involve the use of genes and regulatory circuits that have previously evolved complex roles in an ancestral organism.

Support and deformability in Bethylinae wings

According to Grimaldi & Engel (2005) the venation patterns are important structures for aerodynamic associated with specific flight system and of specialized functional purposes. Thus, the structural adaptations related to support and deformability of the forewings must be mentioned and analyzed to better understand the phylogeny of the bethylines.

The Bethylinae genera as aforementioned display different patterns of cells, veins, flexion lines in their forewings, suggesting that these structures have been played an important role during the evolution of this group by marking differences between forewings in the Bethylinae lineages.

For Wootton (1981), little attention has been given to the functions of wing characters such as the arrangement of veins, thickened areas, fractures and lines of flexion. Moreover, according to him it is usually possible to distinguish areas specialized for deformability, for support and the limiting of deformation.

As aforementioned, the Bethylinae genera always have the C, R, and 1Cu cells closed. The C, Sc and R veins, separate or to some extent fused, almost always together perform a supporting role, at least in the proximal part of the wing. Moreover, M, Cu and RS+M veins can usually form another supporting area when present. Hence, the area containing distal branches of R, Rs, M veins and sometimes of Cu is normally deformable in orthodox membranous wings. Basal fusion of veins is of course common in many insect groups. Hymenoptera provide good examples of the fusion of Sc, R and Rs veins into a single strong, thick vein in the proximal supporting zone of the forewing (Wootton 1981). In the wings the deformable and supporting zones are clearly related functionally to lines of weakness and flexion. Thus, it is reasonable to expect that the structures of the deformable areas might show adaptations to facilitate camber change, optimize the section throughout the area and optimize the pattern of torsion at stroke reversal. Undeniably, the alteration in camber requires flexion along longitudinal or radial axes of the wing. Wootton (1981) stated "*the main veins usually-though not invariably-run more or less radially, and in the absence of cross veins the membranous spaces between them would give ample flexibility*". The flexion lines seem to represent the boundary between the basal supporting areas and the distal deformable area of the remigium.

In this paper two main clades were retrieved, (*Lytopsenella* + *Eupsenella*) (Figs 2, 4) with six closed cells, and ((*Prosierola* + *Odontepyris*) + ((*Sierola* + *Bethylus*) + *"Goniozus"*))) for males (Figs 2, 3), and in the clade ((*Prosierola* + *Odontepyris*) + ((*Sierola* + (*Afrobethylus* + *Bethylus*) + *"Goniozus"*))) for females (Figs 4, 5) with three, four or five closed cells.

Here, we suggest practicable approaches to functional morphology to the venation in the Bethylinae clades. We postulate that probably the pattern displayed of six closed cells in (*Lytopsenella* + *Eupsenella*) (Figs 2, 4) represent an important structural adaptation that plays a role mainly to support the flight. We suggests that probably *Lytopsenella* and *Eupsenella*

can have longer flights than other genera of bethylines, and lower capacity of maneuverability and deformability of their forewings.

The clade ((*Prosierola* + *Odontepyris*) + ((*Sierola* + (*Afrobethylus* + *Bethylus*) + *"Goniozus"*))) (Figs 4, 5) has tree, four and five closed cells in the forewing. This pattern displayed represents structural adaptations mainly to deformability within the deformable areas. About this, Wootton (1981) mentioned that the structure of the deformable areas might show adaptations to facilitate optimize the section throughout the area, camber change, and optimize the pattern of torsion at stroke reversal.

The deformable areas of these groups of rather have entirely lack cross veins. Wootton (1979) named the longitudinal line of weakness in the remigium as median flexion line. Based on this scenario, probably the flexion line seems to represent an important the boundary between the basal supporting areas and the distal deformable area of the remigium. Hence, based on adaptations within the deformable areas of ((*Prosierola* + *Odontepyris*) + ((*Sierola* + (*Afrobethylus* + *Bethylus*) + *"Goniozus"*))) (Figs 4, 5) we can be able to identify clearly the higher capacity of maneuverability, and deformability of their forewings.

Moreover, in the most species of this clade we can observe the stigma large. The species, which possess one, probably may act helping to maintain an aerodynamically useful profile passively, probably also as an inertial regulator of forewing pitch, and angle of attack during the flapping cycle. It is worth mentioning that the most successful in the attack to the hosts, mainly lepidopterous larvae are found in these lineages. This result should not be considered as surprisingly especially if we take into account the most capacity of maneuverability, deformability, and aerodynamics during the flight. Such conditions certainty can contribute decisively with the most precision and accuracy observed by these lineages in the attack to the hosts.

Sierola contains the most of their described species from Hawaii, with three endemic species in Australia. The genus has tremendous speciation in Hawaii, and a secondary small speciation in the Marquesas Islands. This genus differently of the others has five closed cells the first radial (1R1) cell opened. It shown the same pattern of flexion lines of (*Lytopsenella* + *Eupsenella*), that have six closed cells. How to explain this similarity of these two clades in opposite position in tree under evolutionary perspective?

The answer to this question starts understanding the extraordinary geographic isolation of the Hawaiian archipelago (more than 3500 km from the nearest mainland). The Hawaiian

Islands have long been recognized for the spectacular diversity and endemism of their biota (Simon 1987).

Based on this scenario, Gillespie et al. (2001) mentioned that the Pacific Ocean islands display a broad spectrum of geographical attributes, with continental fragments, volcanic hot-spots, and atolls scattered across a huge range of isolation.

Thus, given that evolution process of *Sierola* is the unique among the Bethylinae genera that happens on a hot spot archipelago, such as Hawaii with the forewing pattern five-closed-cells. The five-closed-cells in *Sierola* can be probably related to the particular adaptation process of these lineages to the Hawaiian archipelago. For a period of several million years each new island served as an active substrate for colonization and diversification. However, all species have the share the same pattern in the forewing. This condition probably is due the *Sierola* to be a recent group within the Bethylinae. The adaptive radiations have played a key role in the evolution of biological diversity of *Sierola.*

Male genitalia

Among animals with internal fertilization, many species have species-specific male genitalia with morphological divergence among closely related species that is often dramatic and complex (Eberhard 1985). Tuxen (1970) emphasized that this pattern is especially evident in insects, and male genitalia are considered one of the most important and useful species-diagnostic characters in insect systematics.

Male genitalia are complex organs that consist of many component structures that are functionally different from each other (Song & Wenzel 2008). They are derived from tissues that differ in embryonic origin (Snodgrass 1931, 1957). The genital evolution of male genitalia is under sexual selection (Eberhard 1985, 2001, 2004b; Arnqvist 1997; Arnqvist & Danielsson 1999; Cordoba-Aguilar 2005; House & Simmons 2005). Additionally, it is generally accepted that male genitalia evolve more rapidly. Moreover, even though genitalia are still among the most widely used characters in insect systematics, there is an idea that the rate of evolution is too rapid for genital characters to be useful in forming clades. However, the male genitalia of Bethylinae cannot be considered as megadiverse and variable as in other subfamilies of Bethylidae, but even with this peculiarity we included some characters of male genitalia by the first time in the phylogenetic context to Bethylinae. However, the usage of male genitalia as source of characters in phylogenetic reconstruction for Bethylinae genera is important to retrieved accurately synapomorphies for the Bethylinae lineages.

One of the most conspicuous differences in the male genitalia of Bethylinae species is the number of parameres. Here, male genitalia with two parameres (Fig. 8F) were retrieved as synapomorphy supporting the following clades: (*Lytopsenella* + *Eupsenella*), *Prosierola* and *Bethylus*. Moreover, male genitalia with ventral projection of apical lobe of aedeagus (Fig. 8H) was also retrieved as synapomorphy of the clade ((*Sierola* + *Bethylus*) + *"Goniozus"*).

The previous phylogenetic analyses performed for Bethylinae (Figs 9A-D) did not included genital characters, which are now considered critical to recognize the species of most Bethylidae genera. Azevedo (2003) mentioned that in Bethylidae the male genitalia vary profoundly even in species phylogenetically related. Based on this scenario, use the male genitalia with source of characters in Bethylinae can contribute and to represent the first step to open a new frontier of characters in this subfamily. Moreover, from these characters can improve the accuracy and understanding of the diagnostic characteristics in Bethylinae genera.

Female genitalia

There are few studies on Bethylidae female genitalia such as Evans (1969) and Sorg (1988), but none of them described the ovipositor apparatus. None previous author proposed any character of female genitalia for phylogenetic reconstruction in the Bethylinae species. However, Ramos & Azevedo (2016) drown attention to this issue and described the female genitalia of all species of *Afrobethylus*.

According to Carpenter (1986), Vilhelmsen (2000), and Ernst et al. (2013) some ovipositor apparatus characteristics are phylogenetic signal and help us to understand functional morphology and evolution of apocritan Hymenoptera.

Here, six characters of female genitalia were analyzed, three of them were retrieved as synapomorphies, namely presence of furcula V-shaped (Fig. 8N), presence of proximal projection of second valvifer (2vf) (Fig. 8O) and proximal projection of second valvifer broadly enlarged (Fig. 8Q).

According to Hermann & Chao (1983) the furcula varies considerably among the aculeate wasps in the size, shape and muscle association. Furcula V-shaped (Fig. 8N) was retrieved as a new synapomorphy in subfamily level, as well as the presence of proximal projection of second valvifer (Fig. 8O). This structure is located in the proximal region of second valvifer in all Bethylinae genera, and varies in the size, shape, thickness and curvature. It is slender to

broadly enlarged (Fig. 8Q), as shown in *Afrobethylus*. The proximal projection of second valvifer broadly enlarged was retrieved as synapomorphy to *Afrobethylus* (Fig. 5G).

Conclusions

The present study is the most comprehensive cladistic treatment dedicated to the understanding of the evolution of the Bethylinae genera, and the first to treat consider a global sampling of species of this subfamily.

Our comprehensive taxonomic sampling and use of characters traditionally neglected provided evidence to support the monophyly of seven of the eight extant Bethylinae genera, and explore the importance of selected morphological characters, mainly of male and female genitalia. Moreover, the polytomy unresolved between *Lytopsenella* and *Eupsenella* with all other Bethylinae genera is now solved.

The morphological characters unexplored of male and female genitalia might offer additional data relevant to more robustly estimate the phylogenetic history of this group. These strongly supported results will serve as framework for future studies focused on proposing a stable and predictive classification of genera within Bethylinae. The study both male and female genitalia contributes to improve comprehension of genital evolution in Bethylinae.

In this paper, we promote a first step to direct and encourage future research using the arrangement of forewing veins, flexion lines and male and female characters to phylogenetic reconstruction in Bethylidae.

Ancestral state reconstructions showed that Bethylinae are a phenotypically variable lineage and there are characters that became fixed in their major lineages.

Finally, *Goniozus* claims for a world alpha-taxonomic revision and then phylogenetic studies.

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List of figures

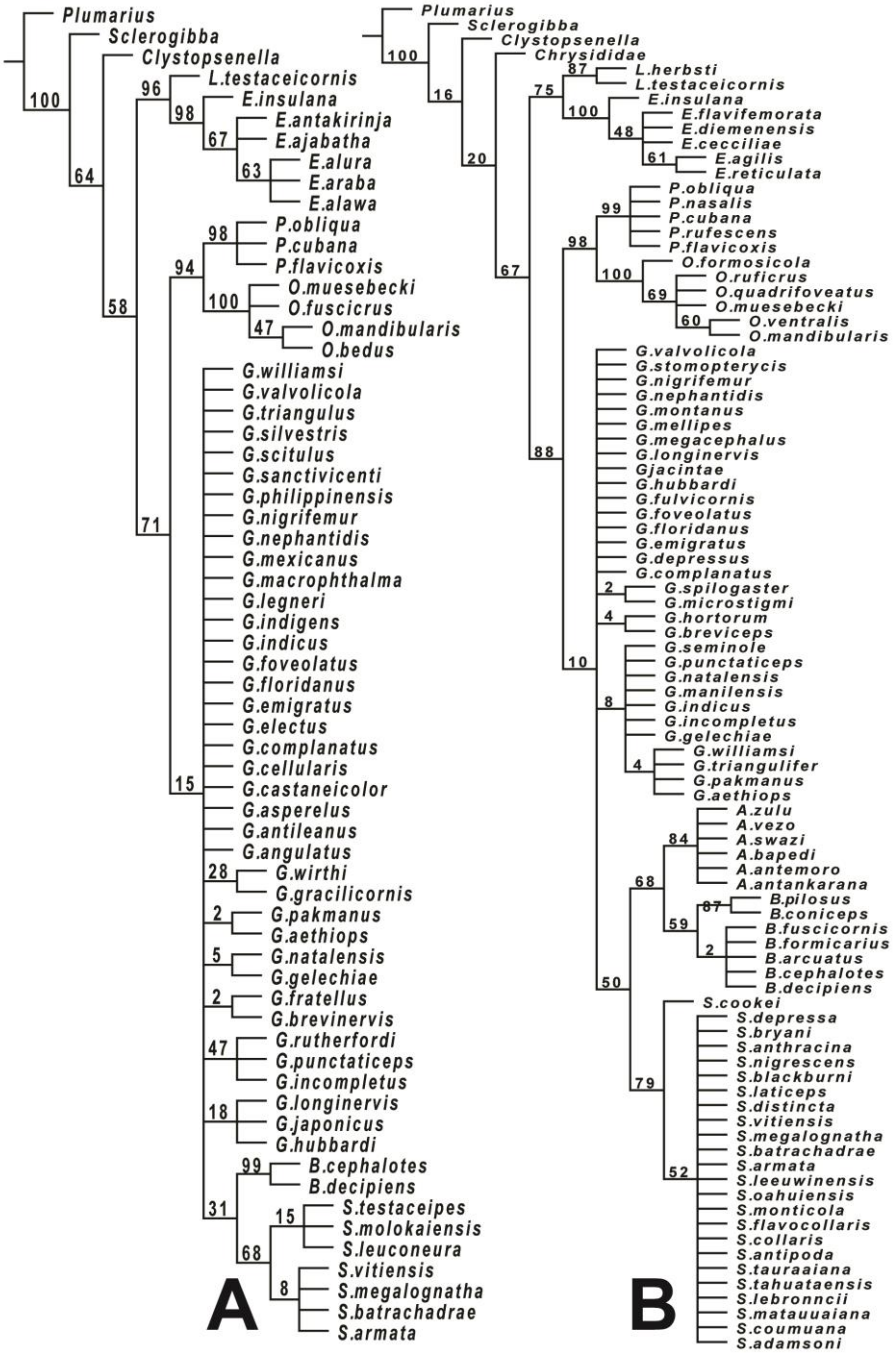

Fig. 1. Major lineages within Bethylinae. A-B. A, strict consensus of seven most parsimonious trees obtained in TNT for the analysis of morphological data for males. Cladogram obtained under implied weighting of the characters (k = 8.906250); B, strict consensus of three most parsimonious trees obtained in TNT for the analysis of morphological data for females. Cladogram obtained under implied weighting of the characters (k = 13.349610) Numbers above the branches are symmetrical resampling support values.

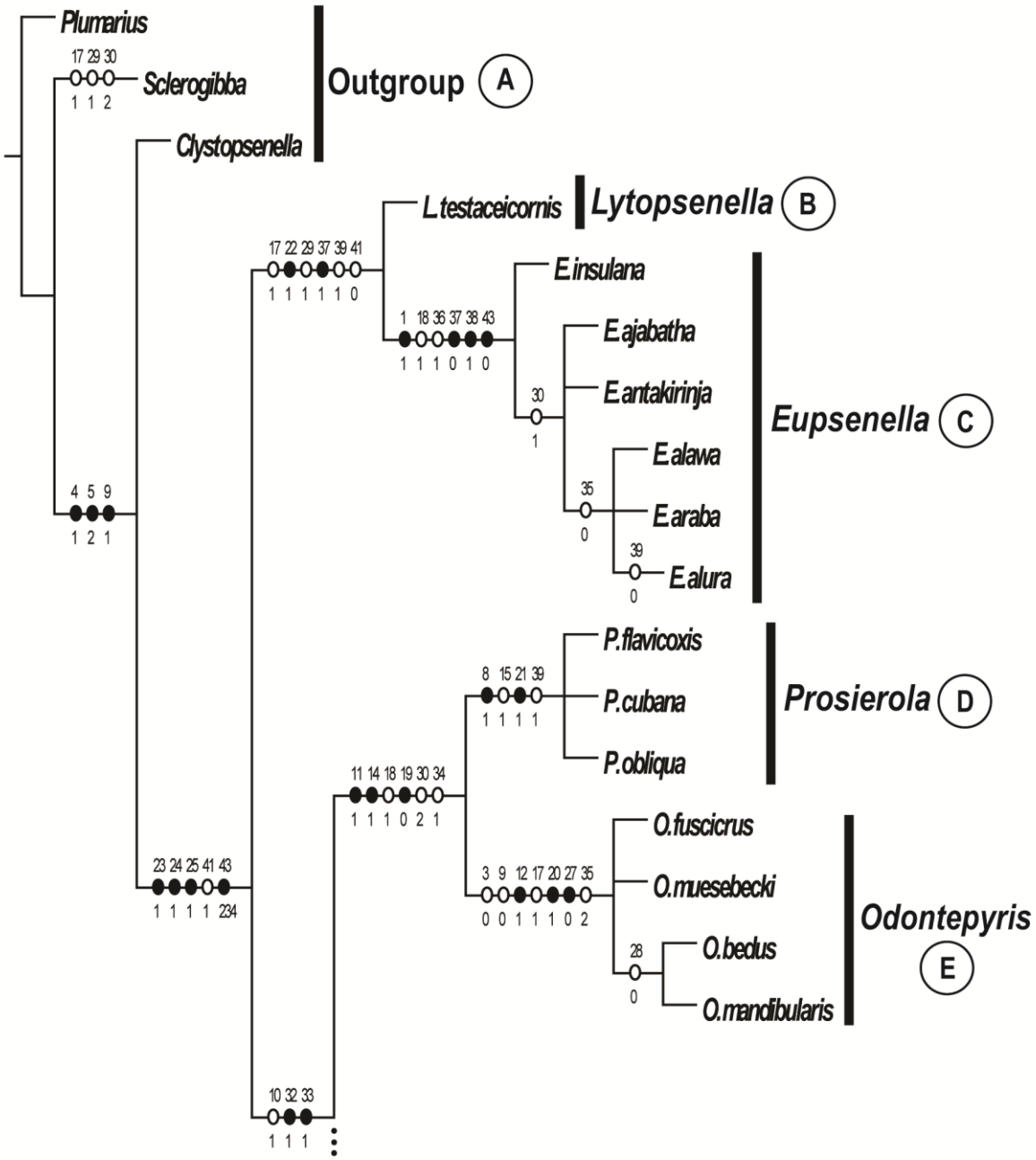

Fig. 2. Portion of the tree based on males showing the sister-group relationship between (*Lytopsenella* + *Eupsenella*) and (*Prosierola* + *Odonteyris*). Cladogram obtained under implied weighting of the characters (k = 8.906250).

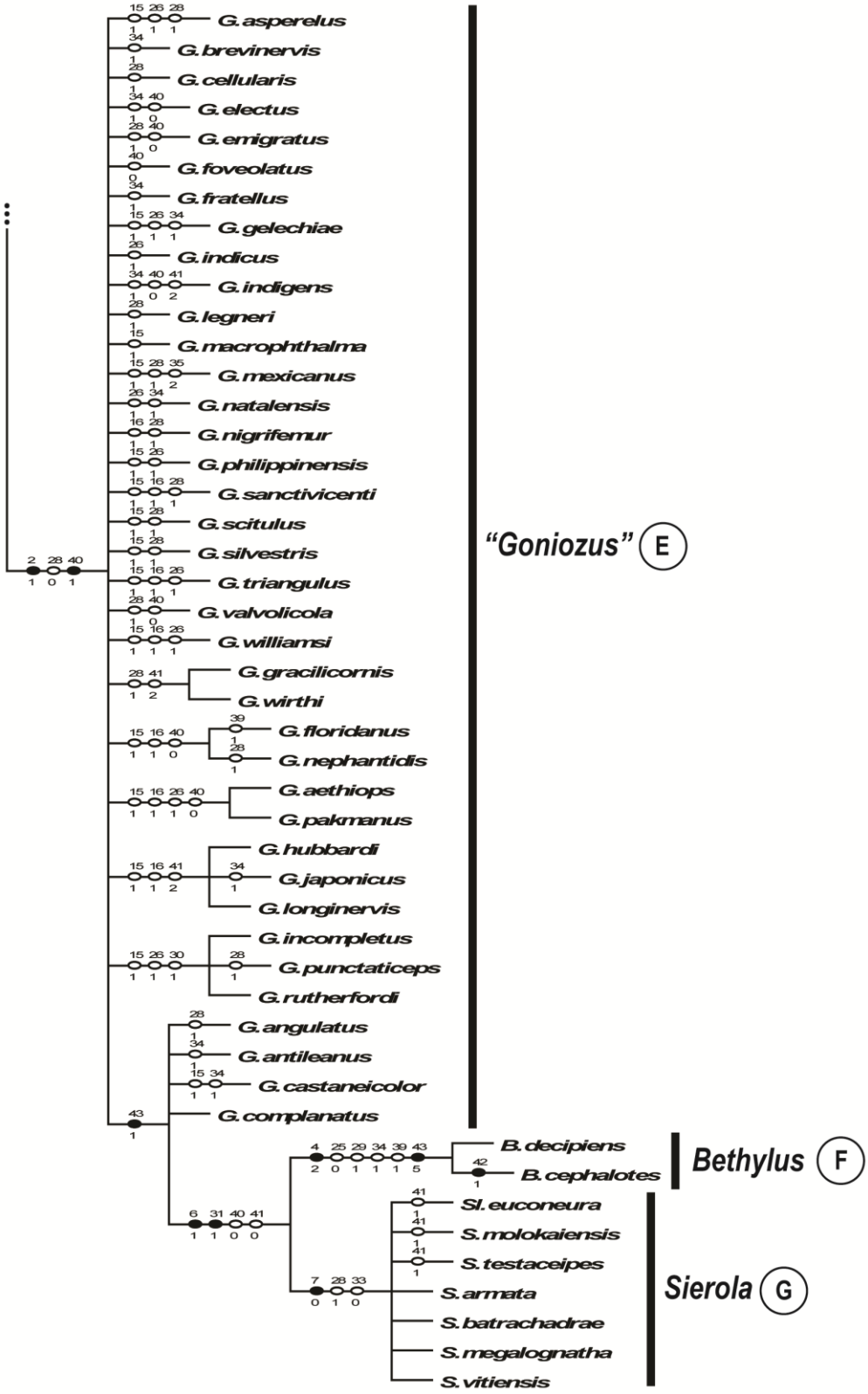

Fig. 3. Portion of the tree based on males showing the sister-group relationship between "*Goniozus*" and (*Bethylus* + *Sierola*). Cladogram obtained under implied weighting of the characters (k = 8.906250).

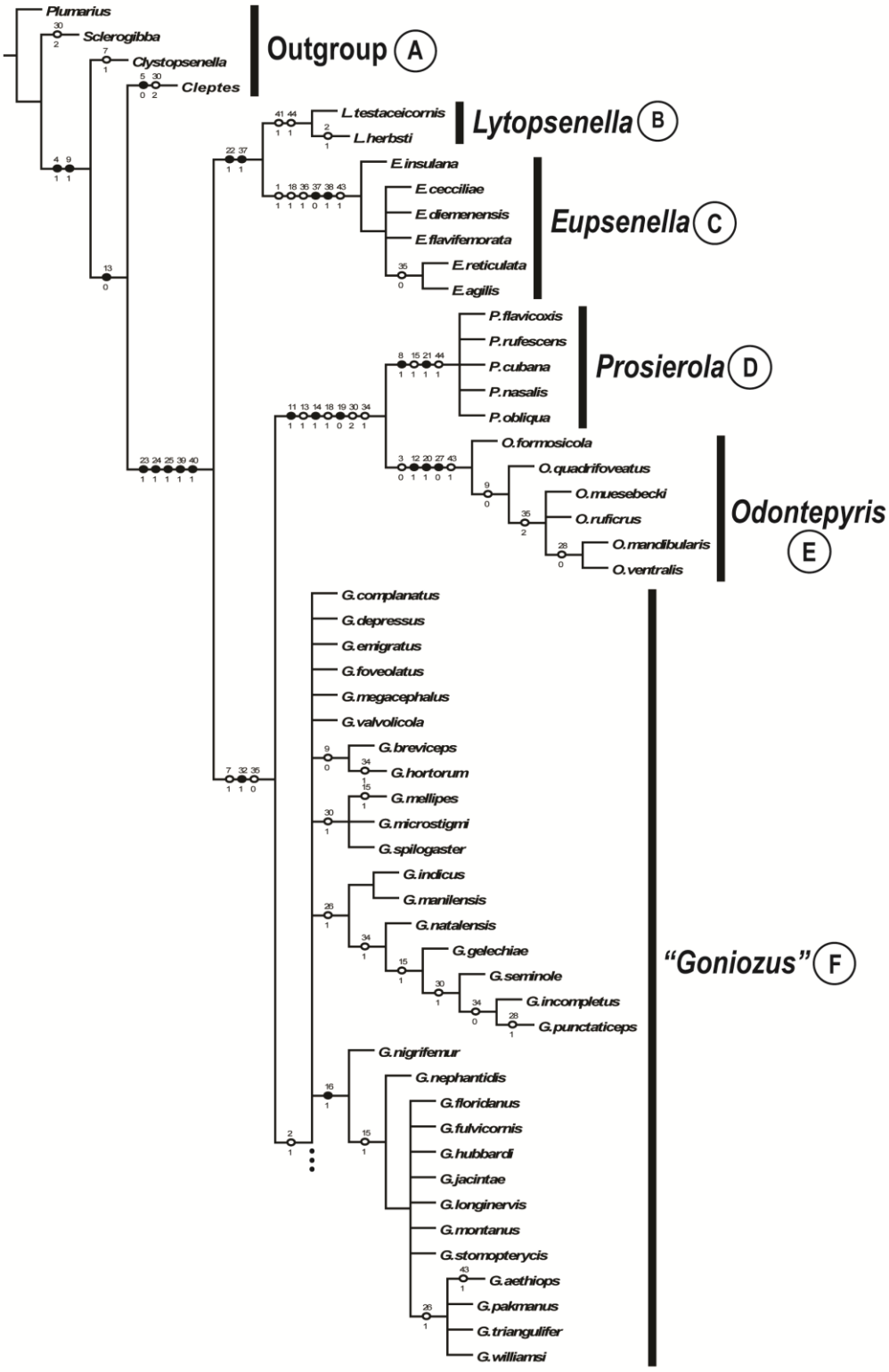

Fig. 4. Portion of the tree based on females showing the sister-group relationship between (*Lytopsenella* + *Eupsenella*), (*Prosierola* + *Odonteyris*) and "*Goniozus*". Cladogram obtained under implied weighting of the characters (k = 13.349610).

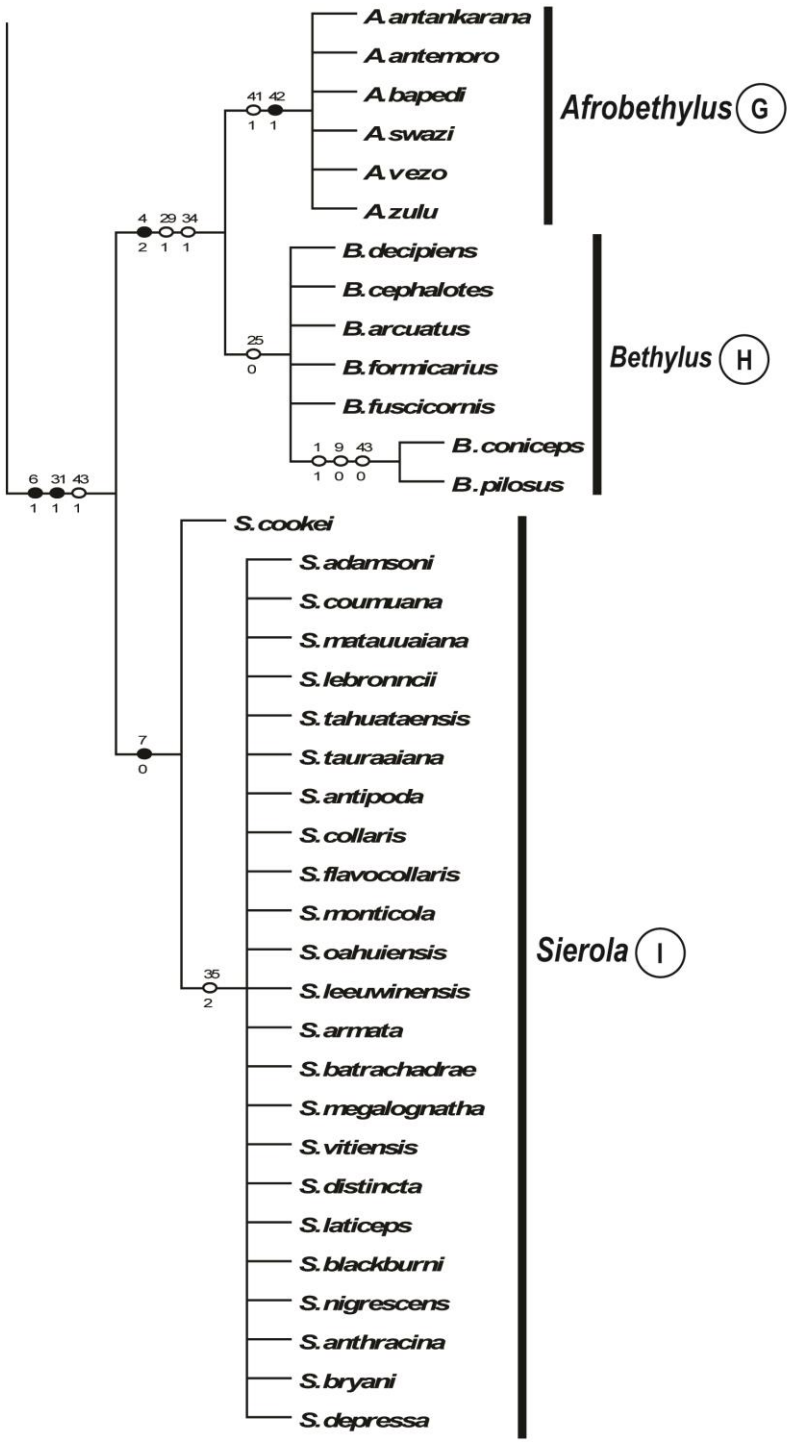

Fig. 5. Portion of the tree based on females showing the sister-group relationship between (*Afrobethylus* + *Bethylus*) and *Sierola*. Cladogram obtained under implied weighting of the characters (k = 13.349610).

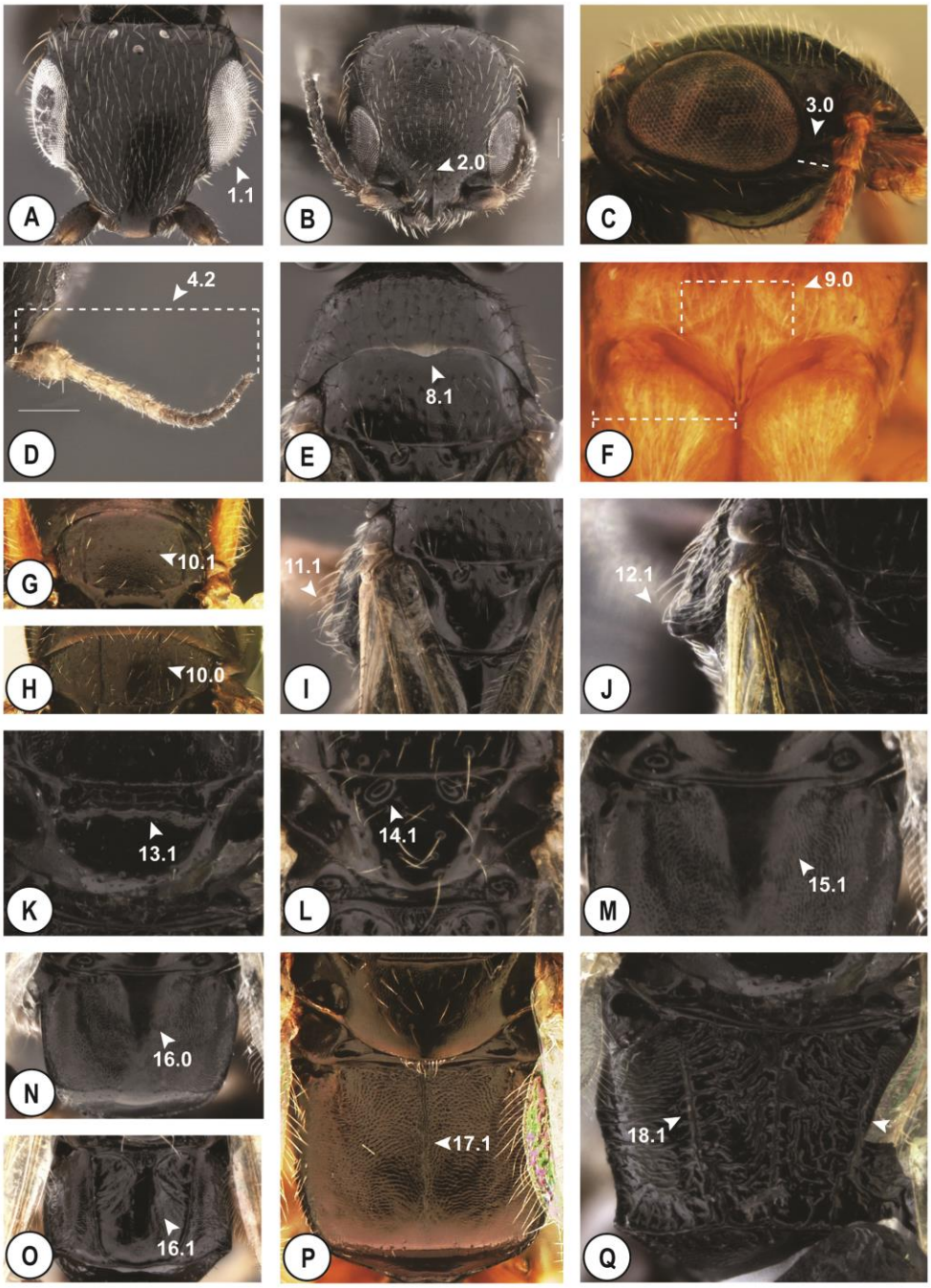

Fig. 6. Characters analyzed here. A-D. Head in dorsal view. A, eye hairy; B, unsculptured streak frontally absent; C, malar space visible; D, antenna with 10 flagellomeres. E. Pronotum in dorsal view. E, posterior margin slightly produced backward medially. F. Prosternum in ventral view. F, smaller than area of forecoxa. G-H. Mesoscutum in dorsal view. G, notaulus absent; H, notaulus present. I-J. Mesopleuron in dorsal view. I, gibbous; J, dentate process present. K-L. Mesoscutellum in dorsal view. K, mesoscutellar groove or pits present as sulcus; L, mesoscutellar fovea enlarged. M-P. Metapostnotum in dorsal view. M, triangular area marked dorsal smooth present; N, triangular area up to the half propodeal disc length; O, triangular area beyond the half propodeal disc length; P, median metapostnotal carina present. Q. Metapectal-propodeal complex in dorsal view. Q, metapostnotal-propodeal suture: conspicuous.

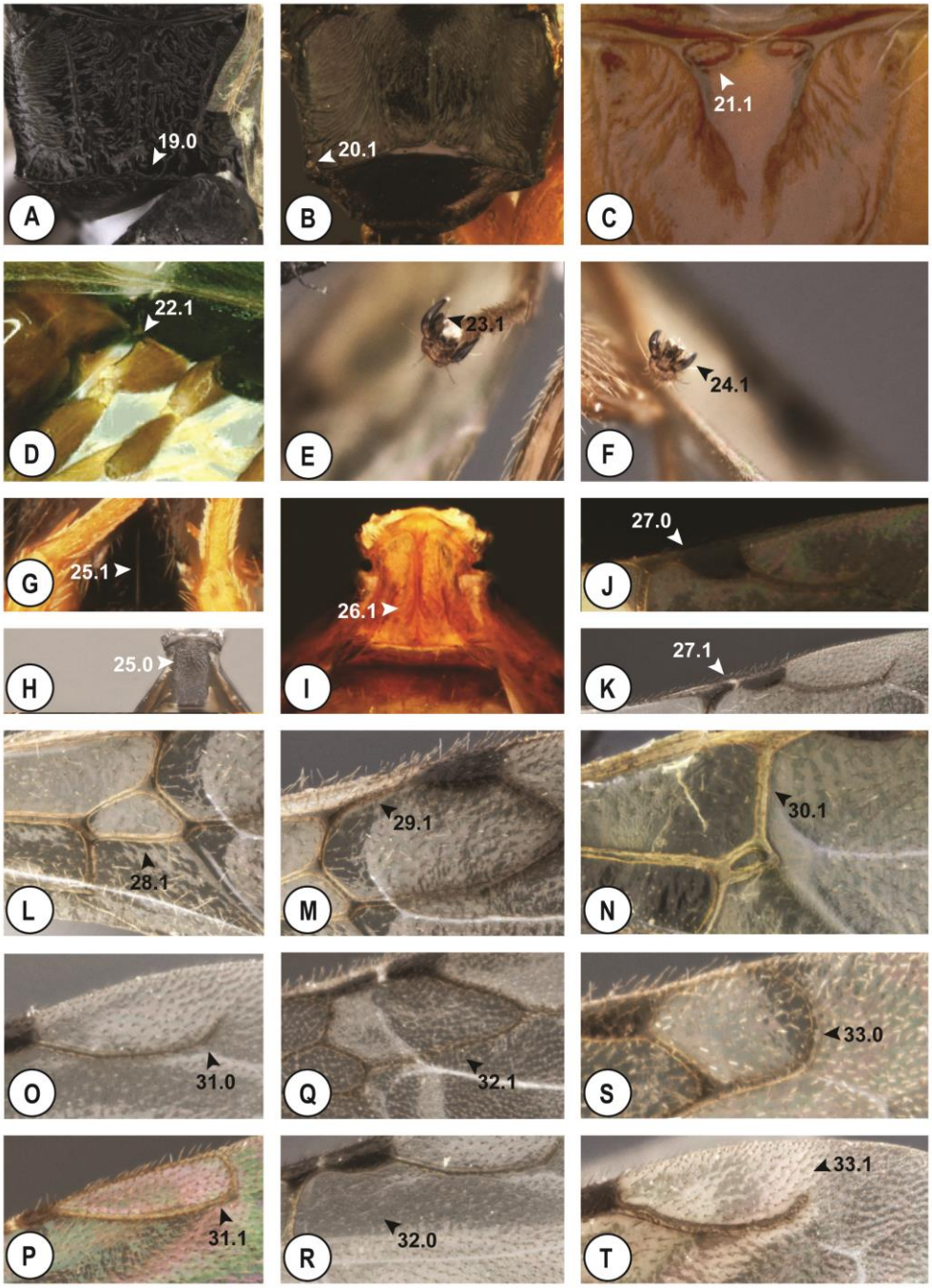

Fig. 7. Characters analyzed here. A-B. Propodeum in dorsal view. A, posterior transverse carina present; B, a pair of pits in basal outer portion of propodeum present. C. Metapostnotum in dorsal. C, a pair of conspicuous anterior pits present. D-F. Legs in dorsal view. D, metacoxae with a large blunt spine; E, two tarsal claws; F, tarsal claws strongly curved. G-I. Petiole in ventral view. G, ventral carina straight present; H, ventral carina absent; I, ventral carina bifurcated posterad. J-T. Right forewing. J, bula absent; K, bula present; L, 2Cu vein present; M, 1R1 vein ill developed; N, 1Rs vein longer than M vein; O, distal margin of Rs vein without a sharp angle; P, distal margin of Rs vein with a sharp angle; Q, first radial cell present; R, first radial cell absent; S, second radial cell closed; T, second radial cell open.

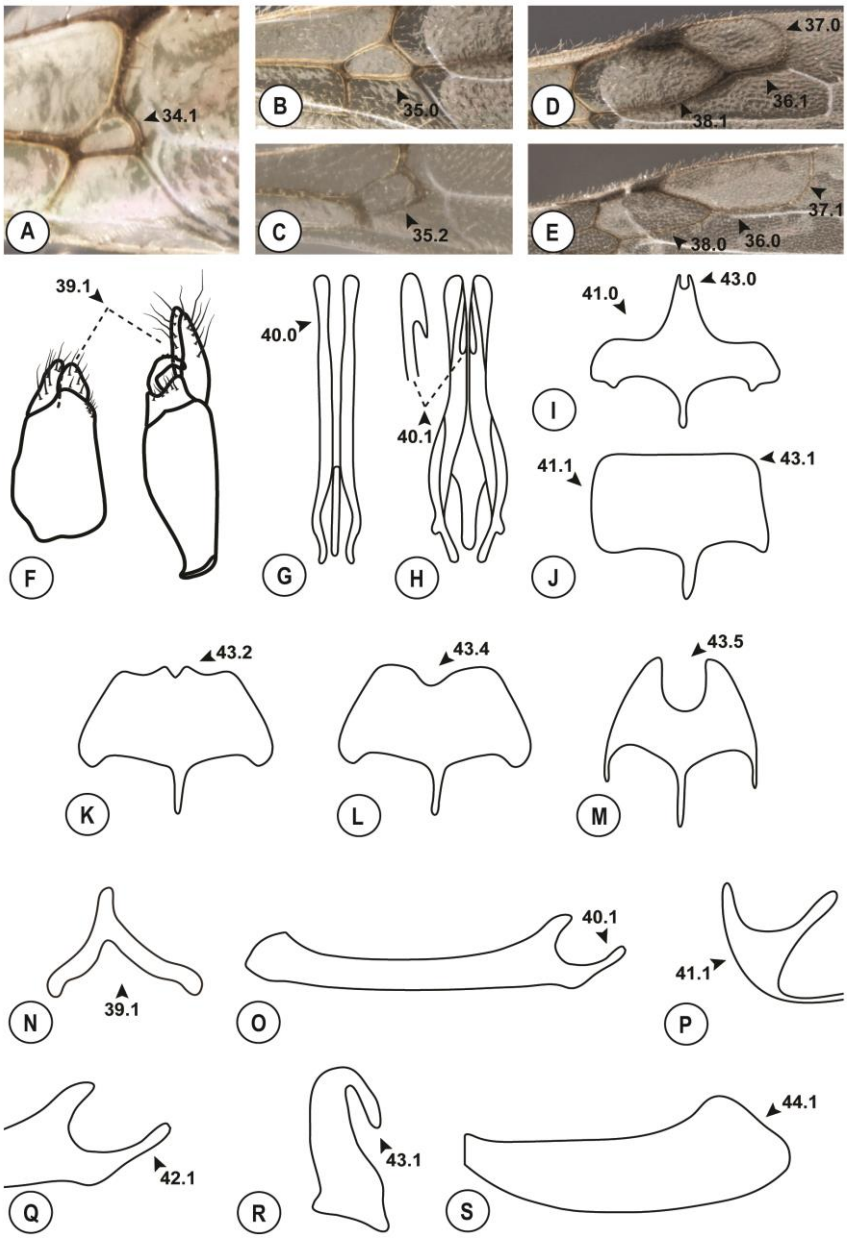

Figure 8. Characters analyzed here. A-E. Right forewing. A, RS+M vein shorter than 1Rs vein; B, first medial cell (areolet) triangular; C, first medial cell (areolet) rectangular; D, second radial cell short (char. 36.1), elliptical (char. 37.0), and first radial cell longer than second radial cell (char. 38.1); E, second radial cell long (char. 36.0), lanceolate (char. 37.1), and first radial cell shorter than second radial cell (char. 38.0). F-H. Male genitalia in profile and ventral view. F, two parameres; G, ventral projection of apical lobe of aedeagus absent; H, ventral projection of apical lobe of aedeagus present. I-M. Male hypopygium in dorsal view. I, shape triangular (char 41.0), and posterior margin bidentate (char. 43.0); J, shape rectangular (char. 41.1), and posterior margin straight (char. 43.1); K, posterior margin medially bilobed; L, posterior margin medially concave; M, posterior margin medially strongly concave. N-S. Female genitalia in dorsal and lateral view. N, furcula V-shaped; O, proximal projection of the second valvifer present; P, basal region of second rami valvularum broadly enlarged; Q, proximal projection of the second valvifer broadly enlarged; R, proximal margin of first valvifer angled; S, distal region of dorsal area of the Tergite 9 (T9) enlarged.

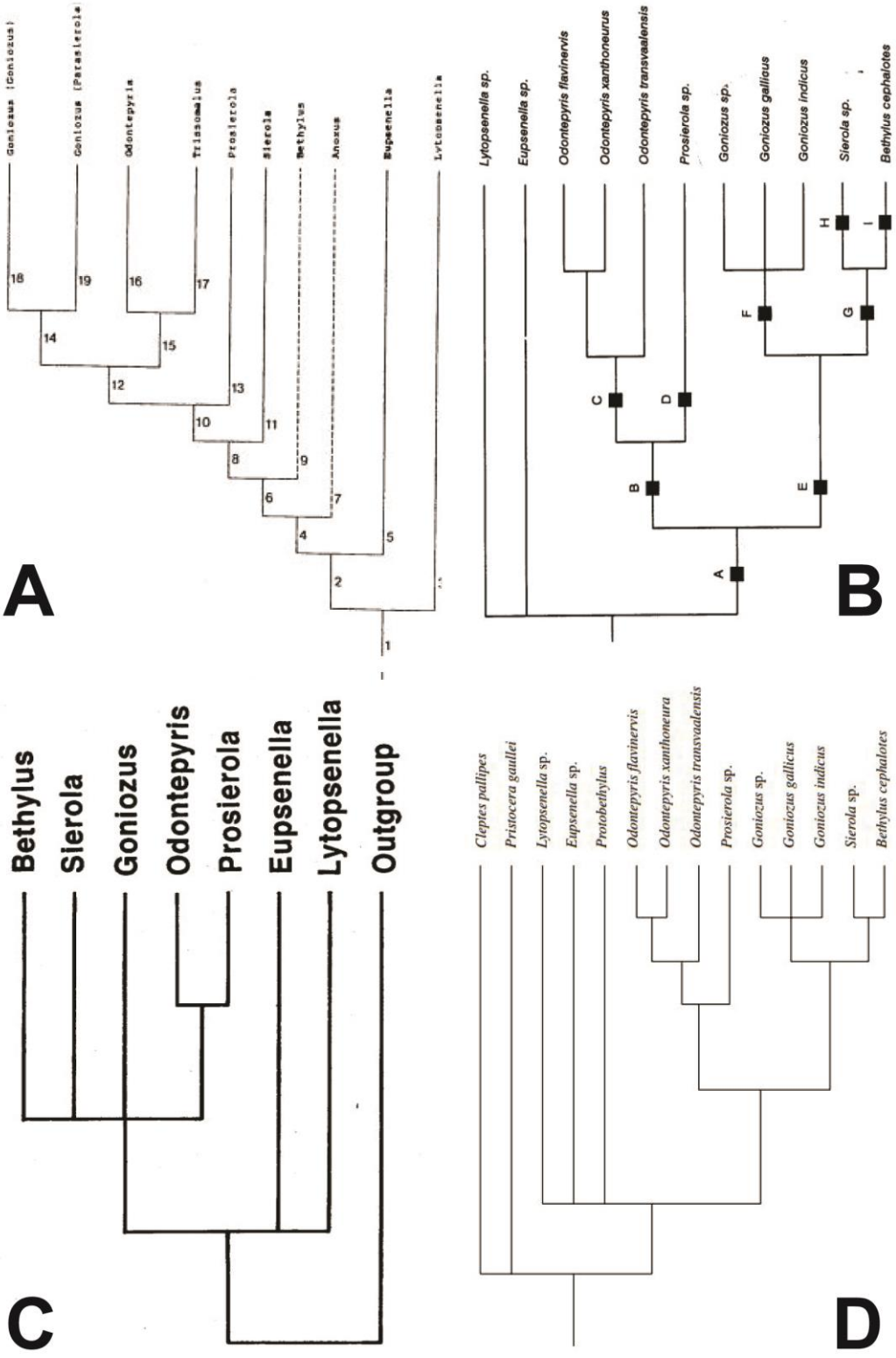

Fig. 9. Phylogenetic hypotheses proposed hitherto for Bethylinae. A-D. A, phylogenetic hypothesis proposed by Sorg (1988); B, phylogenetic hypothesis proposed by Polaszek & Krombein (1994); C, phylogenetic hypothesis proposed by Terayama (1995); phylogenetic hypothesis proposed by De Ploëg & Nel (2004).

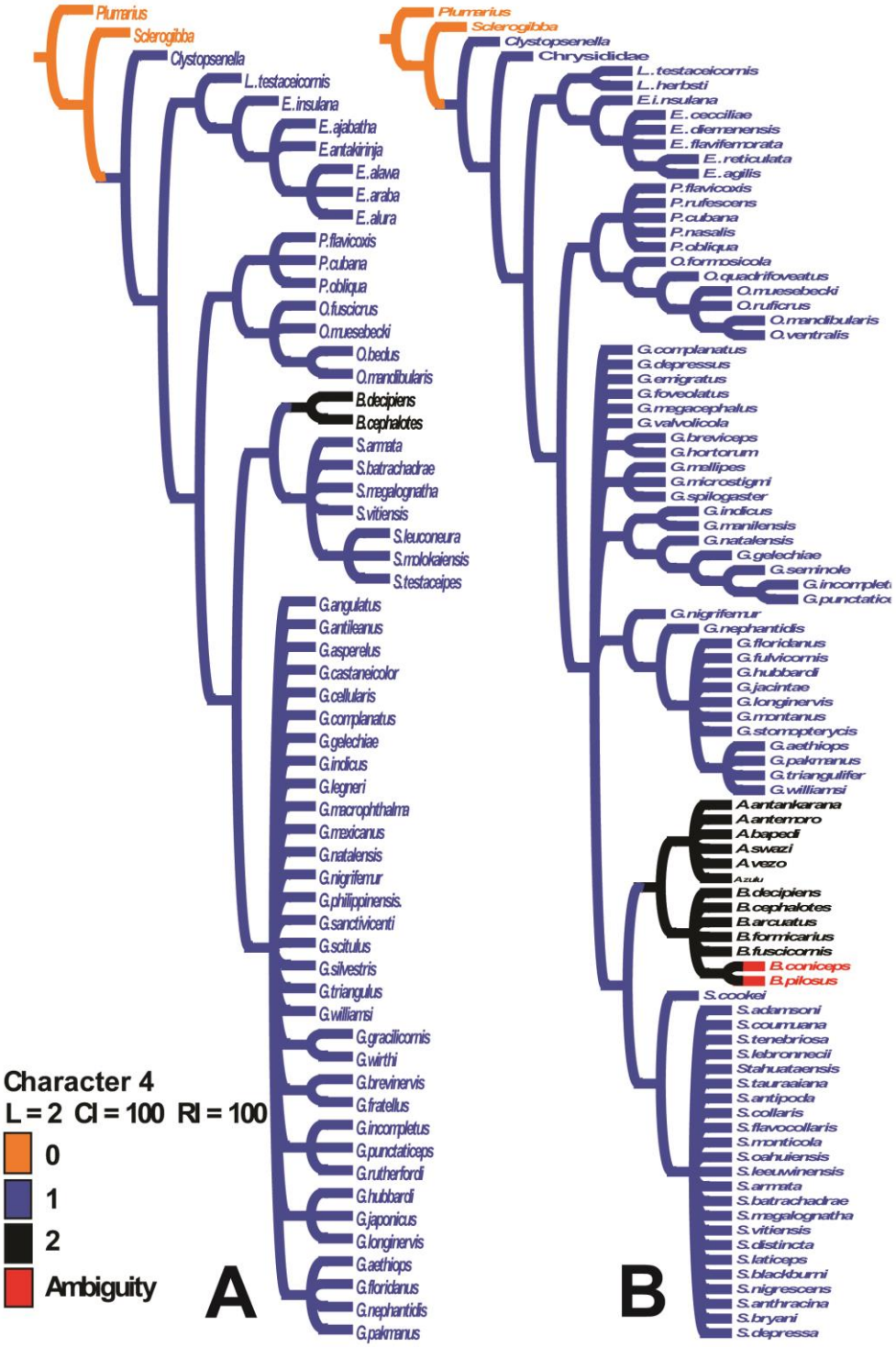

Fig. 10. A-B. A, Ancestral character state reconstruction of the number of flagellomeres for males. Cladogram is the strict consensus tree from most parsimonious analysis of 64 terminals with 43 morphological characters; B, Ancestral character state reconstruction of the number of flagellomeres for females. Cladogram is the strict consensus tree from most parsimonious analysis of 91 terminals with 44 morphological characters.

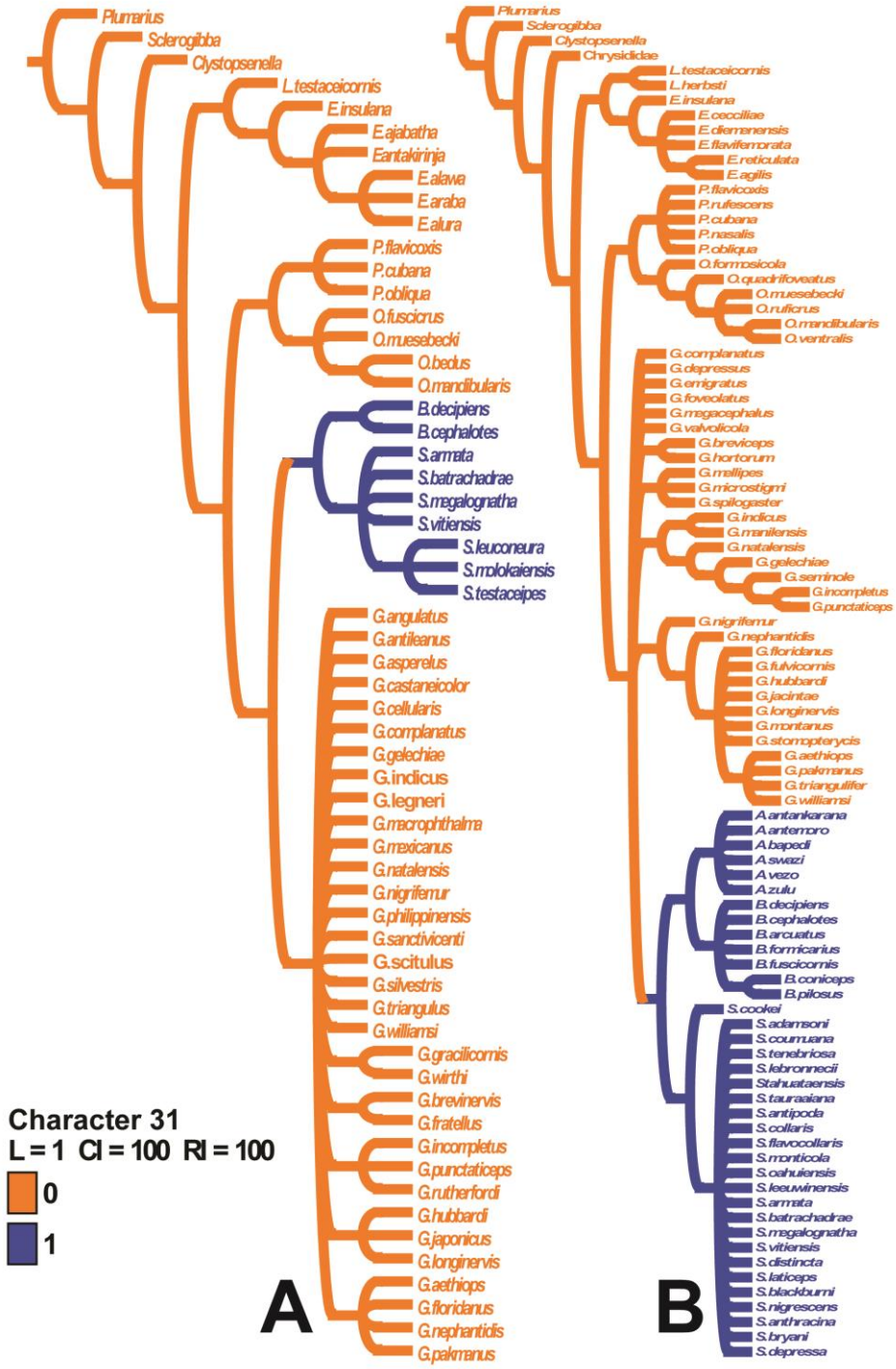

Fig. 11. A-B. A, Ancestral character state reconstruction of angle of distal margin of Rs vein of forewing for males. Cladogram is the strict consensus tree from most parsimonious analysis of 64 terminals with 43 morphological characters; B, Ancestral character state reconstruction of angle of distal margin of Rs vein of forewing for females. Cladogram is the strict consensus tree from most parsimonious analysis of 91 terminals with 44 morphological characters.

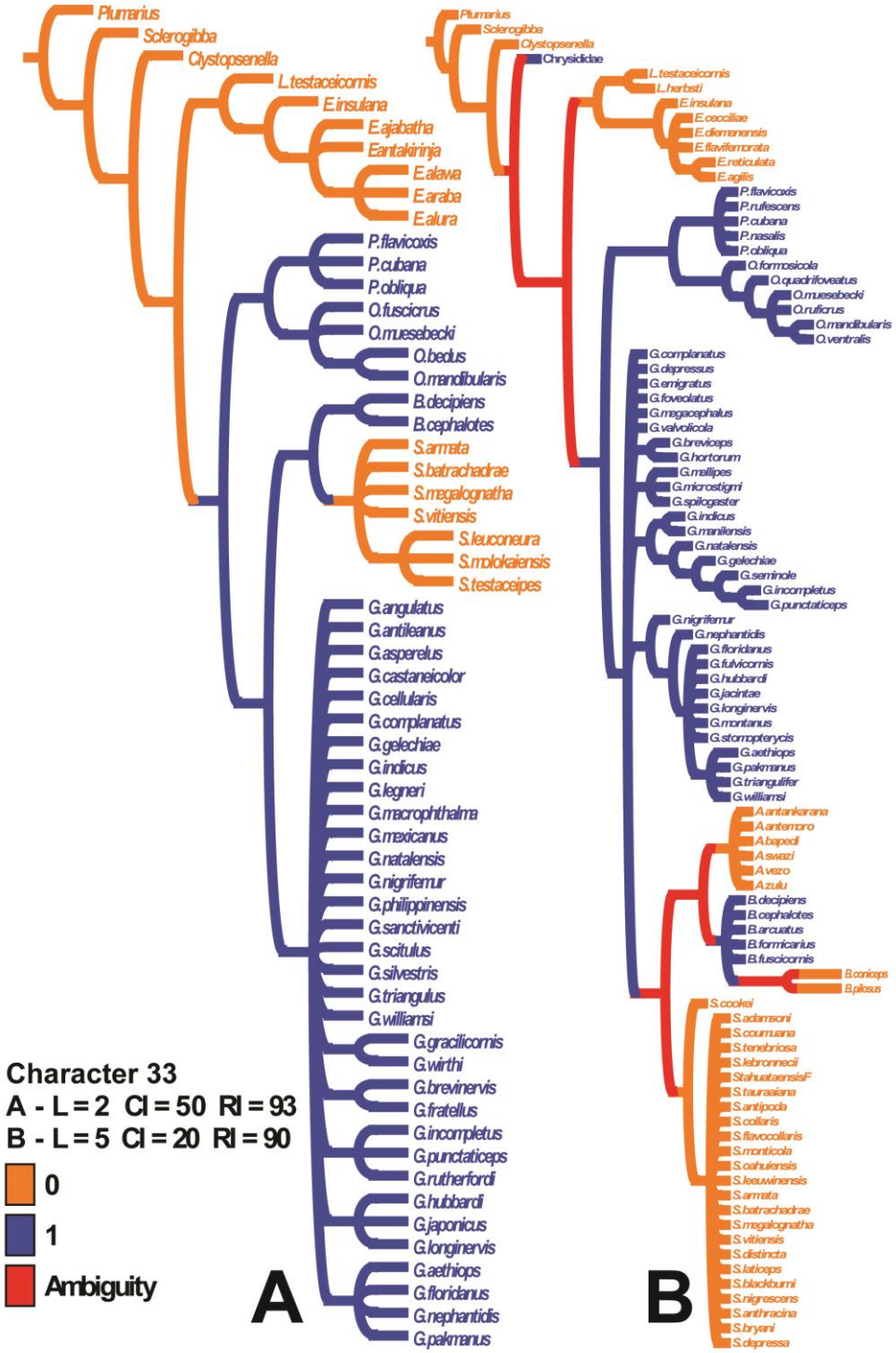

Fig. 12. A-B. A, Ancestral character state reconstruction of second radial cell of forewing for males. Cladogram is the strict consensus tree from most parsimonious analysis of 64 terminals with 43 morphological characters; B, Ancestral character state reconstruction second radial cell of forewing for females. Cladogram is the strict consensus tree from most parsimonious analysis of 91 terminals with 44 morphological characters.

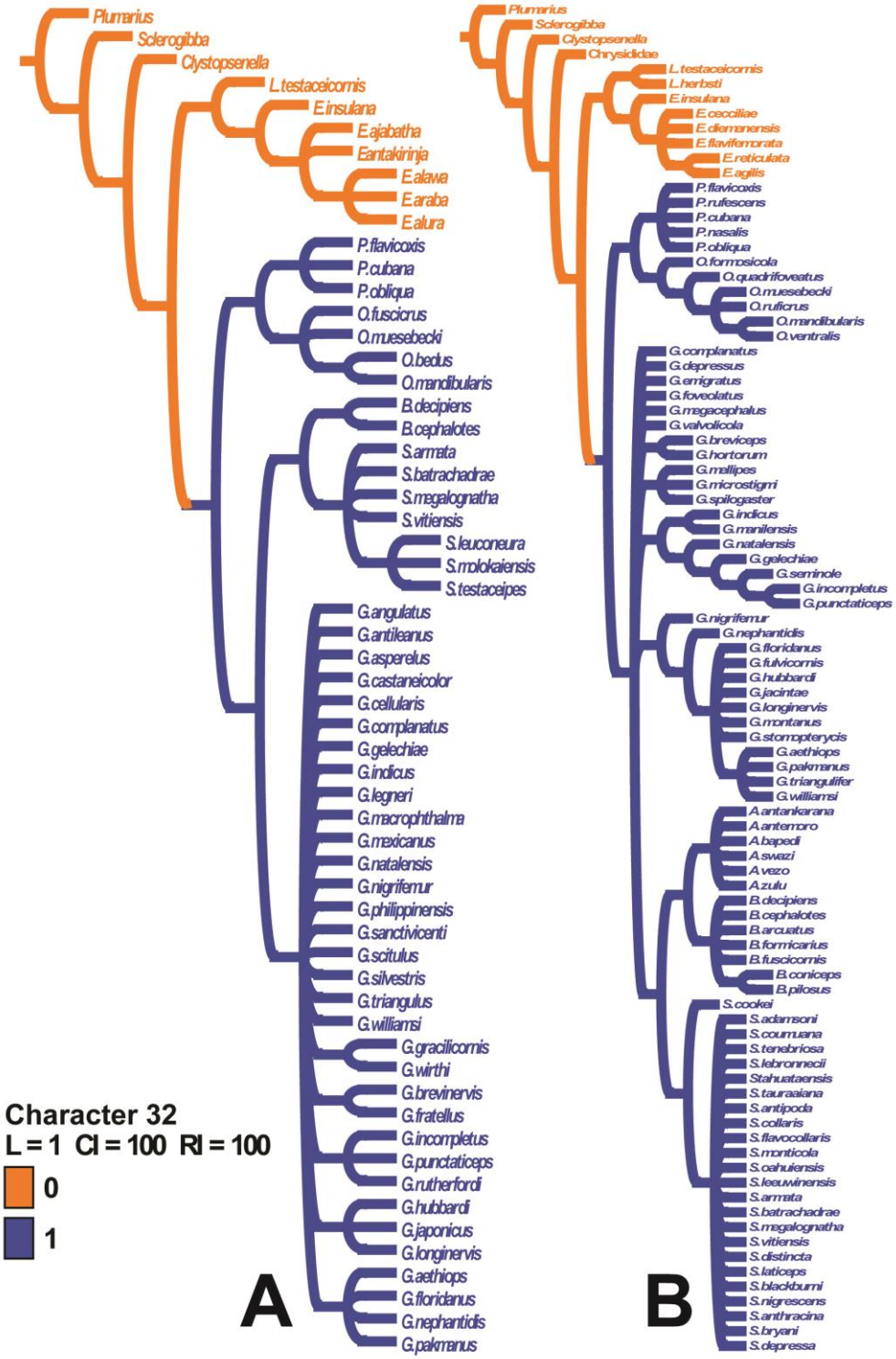

Fig. 13. A-B. A, Ancestral character state reconstruction of first radial cell of forewing for males. Cladogram is the strict consensus tree from most parsimonious analysis of 64 terminals with 43 morphological characters; B, Ancestral character state reconstruction of first radial cell of forewing for females. Cladogram is the strict consensus tree from most parsimonious analysis of 91 terminals with 44 morphological characters.

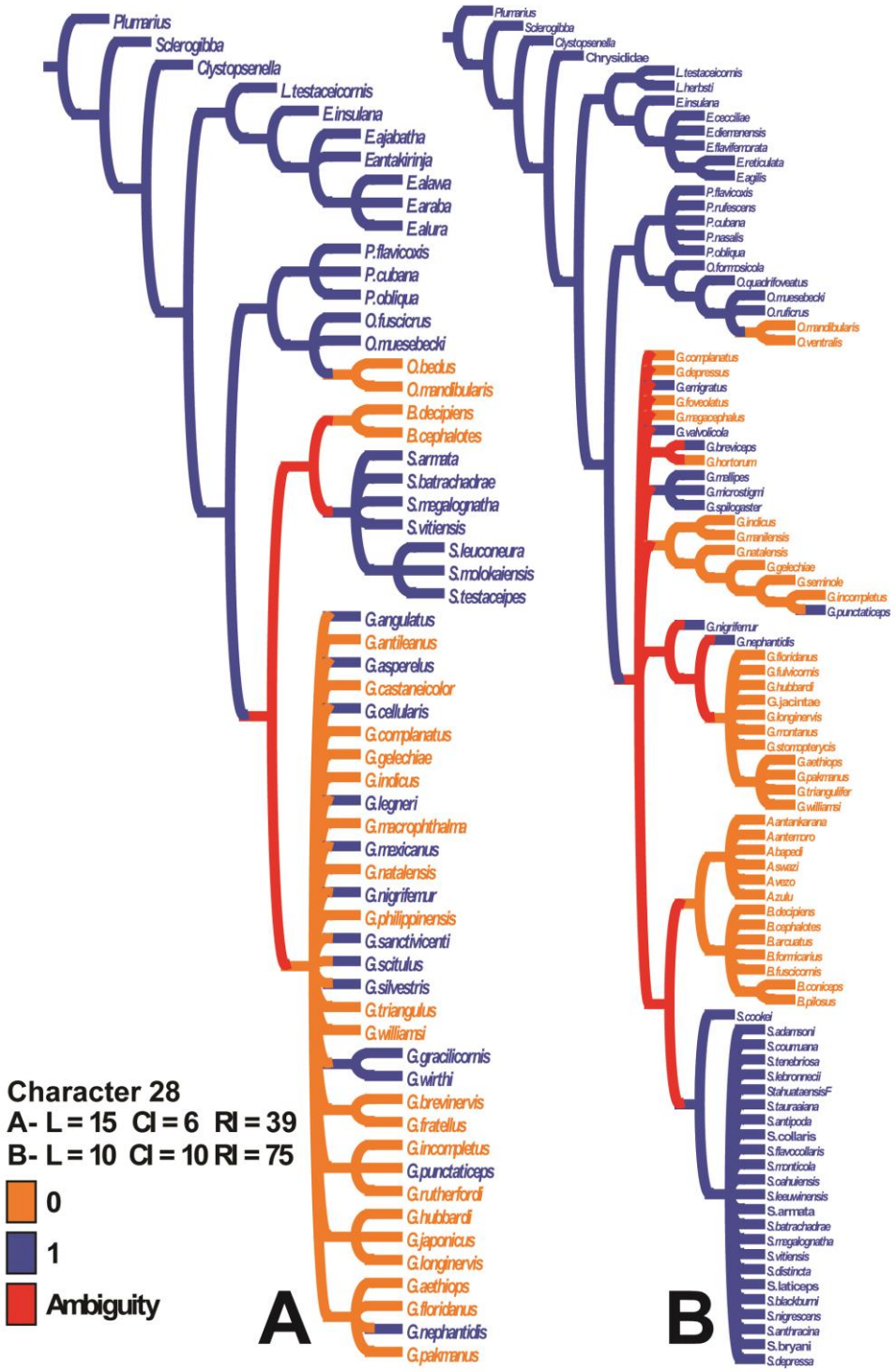

Fig. 14. A-B. A, Ancestral character state reconstruction of 2Cu vein of forewing for males. Cladogram is the strict consensus tree from most parsimonious analysis of 64 terminals with 43 morphological characters; B, Ancestral character state reconstruction of 2Cu vein of forewing for females. Cladogram is the strict consensus tree from most parsimonious analysis of 91 terminals with 44 morphological characters.

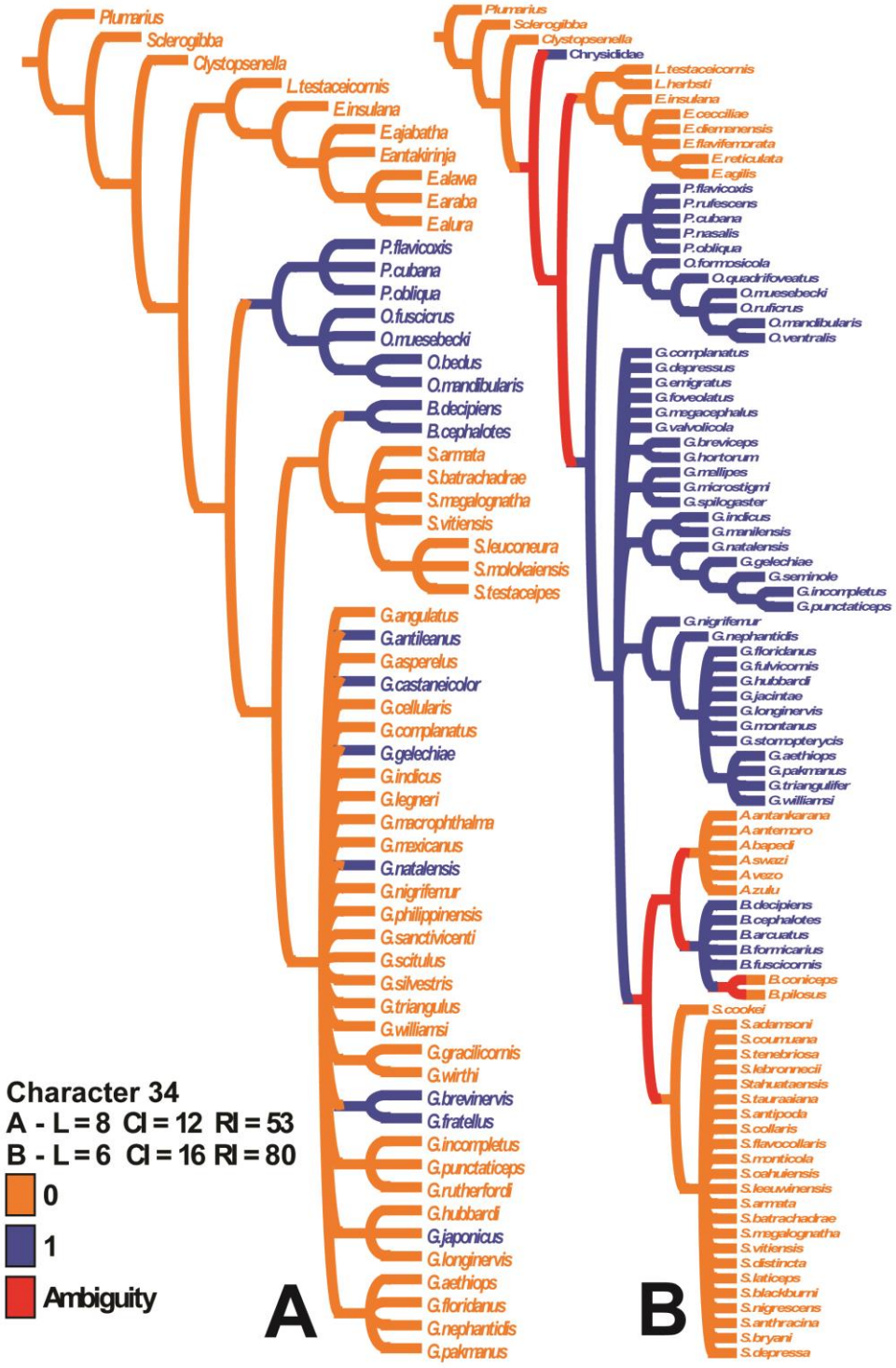

Fig. 15. A-B. A, Ancestral character state reconstruction of RS+M vein of forewing for males. Cladogram is the strict consensus tree from most parsimonious analysis of 64 terminals with 43 morphological characters; B, Ancestral character state reconstruction of RS+M vein of forewing for females. Cladogram is the strict consensus tree from most parsimonious analysis of 91 terminals with 44 morphological characters.

List of tables

Tab. 1. Terminal taxa of morphological analysis used in the present study as outgroup and ingroup, with distribution indicated for each terminal; type-specimens indicated with an asterisk

Taxon	Group		Locality
	Outgroup	Ingroup	
Plumariidae			
Plumarius Philippi	X		Brazil
Scleroggibidae			
Sclerogibba Riggio & De Stefani	X		United Arab Emirates
Scolebythidae			
Clystopsenella Kieffer	X		Costa Rica
Chrysididae			
Cleptes Latreille	X		United States of America
Afrobethylus Ramos & Azevedo			
A. antankarana Ramos & Azevedo*		X	Madagascar
A. antemoro Ramos & Azevedo*		X	Madagascar
A. bapedi Ramos & Azevedo*		X	South Africa
A. swazi Ramos & Azevedo*		X	South Africa
A. vezo Ramos & Azevedo*		X	Madagascar
A. zulu Ramos & Azevedo*		X	South Africa
Bethylus **Latreille**			
B. arcuatus Kieffer		X	Romania
B. cephalotes (Förster)*		X	Germany
B. decipiens (Provancher)*		X	Canada
B. formicarius (Panzer)		X	Germany
B. fuscicornis (Jurine)		X	France
Eupsenella **Westwood**			
E. agilis Westwood		X	Australia
E. ajabatha Ramos & Azevedo		X	Australia
E. alawa Ramos & Azevedo		X	Australia
E. alura Ramos & Azevedo*		X	Australia
E. antakirinja Ramos & Azevedo*		X	Australia
E. araba Ramos & Azevedo*		X	Australia
E. ceciliae Terayama*		X	Australia
E. diemenensis Dodd*		X	Australia
E. flavifemorata Terayama*		X	Australia
E. insulana Gordh & Harris*		X	New Zealand
E. reticulata Terayama*		X	Australia
Goniozus **Förster**			
G. aethiops Evans		X	Ethiopia
G. angulatus (Muesebeck)*		X	Australia
G. antileanus Evans*		X	Dominica
G. asperulus Evans		X	United States of America
G. breviceps (Krombein)*		X	United States of America
G. brevinervis Fouts*		X	United States of America
G. castaneicolor Evans		X	United States of America
G. cellularis (Say)		X	United States of America
G. complanatus Evans*		X	United States of America

Tab. 1. (*Continued*)

Taxon	Group		Locality
	Outgroup	Ingroup	
G. depressus Kieffer		X	Philippines
G. emigratus (Rohwer)*		X	Hawaii
G. floridanus (Ashmead)*		X	United States of America
G. foveolatus Ashmead*		X	United States of America
G. fratellus Evans		X	United States of America
G. fulvicornis (Rohwer)*		X	India
G. gelechiae Evans*		X	United States of America
G. gracilicornis (Kieffer)		X	United States of America
G. hortorum Brues		X	Canada
G. hubbardi Howard*		X	United States of America
G. incompletus Ashmead*		X	St Vincent
G. indicus Ashmead*		X	India
G. jacintae Farrugia*		X	Australia
G. japonicus Ashmead*		X	Japan
G. legneri Gordh*		X	Uruguay
G. longinervis Fouts*		X	United States of America
G. macrophthalma Kieffer		X	Mexico
G. manilensis Kieffer		X	Philippines
G. megacephalus Ashmead*		X	United States of America
G. mellipes (Muesebeck)*		X	India
G. mexicanus Ashmead*		X	Mexico
G. microstigmi Evans		X	Pamama
G. montanus (Motschulsky)		X	India
G. natalensis Gordh		X	South Africa
G. nephantidis (Muesebeck)*		X	India
G. nigrifemur Ashmead*		X	St Vincent
G. pakmanus Gordh		X	United States of America
G. philippinensis Ashmead*		X	Philippines
G. punctaticeps (Kieffer)		X	United States of America
G. rutherfordi Krombein		X	Sri Lanka
G. sanctivincenti Ashmead*		X	St Vincent
G. scitulus Evans*		X	United States of America
G. seminole Evans*		X	United States of America
G. silvestris (Evans)*		X	Dominica
G. spilogaster Evans		X	Cuba
G. stomopterycis Ram & Subba Rao		X	India
G. triangulifer Kieffer		X	Philippines
G. triangulus Kieffer		X	India
G. valvolicola Krombein		X	Sri Lanka
G. williamsi Bridwell		X	Philippines
G. wirthi (Evans)*		X	Dominica

Tab. 1. (*Continued*)

Taxon	Group		Locality
	Outgroup	Ingroup	
***Lytopsenella* Kieffer**			
L. herbsti (Kieffer)		X	Chile
L. testaceicornis (Kieffer)		X	Chile
***Odontepyris* Kieffer**			
O. bedus Alencar & Azevedo*		X	Madagascar
O. formosicola Terayama		X	Taiwan
O. fuscicrus (Kieffer)		X	Australia
O. mandibularis Krombein*		X	Sri Lanka
O. muesebecki Krombein*		X	Sri Lanka
O. quadrifoveatus (Muesebeck)*		X	India
O. ruficrus Krombein*		X	Sri Lanka
O. ventralis Krombein*		X	Sri Lanka
***Prosierola* Kieffer**			
P. cubana Evans*		X	Cuba
P. flavicoxis (Kieffer)*		X	United States of America
P. nasalis (Westwood)		X	Panama
P. obliqua Evans		X	Bolivia
P. rufescens Evans		X	Paraguay
***Sierola* Cameron**			
S. adamsoni Fullaway*		X	Marquesas
S. anthracina Fullaway*		X	Hawaii
S. antipoda Ashmead*		X	Australia
S. armata Fullaway*		X	Hawaii
S. batrachedrae Fullaway*		X	Hawaii
S. blackburni Fullaway*		X	Hawaii
S. bryani Fullaway*		X	Marquesas
S. collaris Ashmead*		X	Hawaii
S. comuana Fullaway*		X	Hawaii
S. cookei Fullaway*		X	Marquesas
S. depressa Fullaway*		X	Hawaii
S. distincta Fullaway*		X	Hawaii
S. flavocollaris Ashmead*		X	Hawaii
S. laticeps Fullaway*		X	Hawaii
S. lebronnecii Fullaway*		X	Hawaii
S. leeuwinensis Turner*		X	Australia
S. leuconeura Cameron*		X	Hawaii
S. megalognatha Fullaway*		X	Hawaii
S. molokaiensis Ashmead*		X	Hawaii
S. monticola Cameron*		X	Hawaii
S. nigrescens Fullaway*		X	Hawaii
S. oahuensis Ashmead*		X	Hawaii
S. tahutaensis Fullaway*		X	Marquesas
S. tauraaiana Fullaway*		X	Marquesas
S. tenebriosa Fullaway*		X	Hawaii
S. testaceipes Cameron*		X	Hawaii
S. vitiensis Fullaway*		X	Hawaii

Tab. 2. Morphological data matrix based on males constructed for the analyses; inapplicable, and unknown states are indicated as ?

Terminals	Characters 1	10	20	30	40	43
Plumarius Philippi	0 0 0 0 0 0 2 0 0 1	0 0 1 0 0 ? 0 0 1	0 0 0 0 0 0 ? 1 1 0	0 0 0 0 0 2 1 2 0 0	0 3 ?	6
Sclerogibba Riggio & De Stefani	0 0 1 0 0 0 2 0 0 0	0 0 1 0 0 ? 1 0 1	0 0 0 0 0 0 ? 1 1 1	2 0 0 0 0 ? 0 2 0 0	0 3 ?	6
Clystopsenella Kieffer	0 0 0 1 1 0 1 0 1 0	0 0 1 0 0 ? 0 0 1	0 0 0 0 0 0 ? 1 1 0	0 0 0 0 0 1 0 ? 0 0	0 3 ?	6
Bethylus cephalotes (Förster)	0 1 1 2 1 1 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 0 ? 1 0 1	0 1 1 1 1 ? 0 2 ? 1	0 0 1	5
B. decipiens (Provancher)	0 1 1 2 1 1 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 0 ? 1 0 1	0 1 1 1 1 ? 0 2 ? 1	0 0 0	5
Eupsenella ajabatha Ramos & Azevedo	1 0 1 1 1 0 2 0 1 0	0 0 0 0 0 ? 1 1 1	0 0 1 1 1 1 0 1 1 1	1 0 0 0 0 1 1 0 1 1	0 0 ?	0
E. alawa Ramos & Azevedo	1 0 1 1 1 0 2 0 1 0	0 0 0 0 0 ? 1 1 1	0 0 1 1 1 1 0 1 1 1	1 0 0 0 0 0 1 0 1 1	0 0 ?	0
E. alura Ramos & Azevedo	1 0 1 1 1 0 2 0 1 0	0 0 0 0 0 ? 1 1 1	0 0 1 1 1 1 0 1 1 1	1 0 0 0 0 0 1 0 1 0	0 0 0	0
E. antakirinja Ramos & Azevedo	1 0 1 1 1 0 2 0 1 0	0 0 0 0 0 ? 1 1 1	0 0 1 1 1 1 0 1 1 1	1 0 0 0 0 1 1 0 1 1	0 0 ?	0
E. araba Ramos & Azevedo	1 0 1 1 1 0 2 0 1 0	0 0 0 0 0 ? 1 1 1	0 0 1 1 1 1 0 1 1 1	1 0 0 0 0 0 1 0 1 1	0 0 ?	0
E. insulana Ramos & Azevedo	1 0 1 1 1 0 2 0 1 0	0 0 0 0 0 ? 1 1 1	0 0 1 1 1 1 0 1 1 1	0 0 0 0 0 1 1 0 1 1	0 0 0	0
Goniozus aethiops Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 0	0 1 0	2
G. angulatus (Muesebeck)	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1 0	1
G. antileanus Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? ?	1 1 0	1
G. asperelus Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1 0	2
G. brevinervis Fouts	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 0	1 1 0	2
G. castaneicolor Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 0	1 1 0	1
G. cellularis (Say)	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 0 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1 0	2
G. complanatus Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 0 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 1 0	1
G. electus Fouts	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 0	0 1 0	2
G. emigratus (Rohwer)	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	0 1 0	2
G. floridanus (Ashmead)	0 1 1 1 1 0 1 0 1 1	0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	0 1 0	2
G. foveolatus Ashmead	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 0	0 1 0	2
G. fratellus Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 0	1 1 0	2
G. gelechiae Evans	0 1 1 1 1 0 1 0 1 1	0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 1 ? 0 ? ? 0	1 1 0	2
G. gracilicornis (Kieffer)	0 1 1 1 1 0 1 0 1 1	0 0 0 0 0 0 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 2 0	2
G. hubbardi Howard	0 1 1 1 1 0 1 0 1 1	0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 2 0	2

Tab. 2. (*Continued*)

Terminals	Characters 1	10	20	30	40	43
G. incompletus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	1 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. indicus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 0 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. indigens Evans	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 0	0 2	0 2
G. japonicus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 0	1 2	0 2
G. legneri Gordh	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1	0 2
G. longinervis Fouts	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 2	0 2
G. macrophthalma Kieffer	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. mexicanus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 2 0 ? ? 0	1 1	0 2
G. natalensis Gordh	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 1 ? 0 ? ? 0	1 1	0 2
G. nephantidis (Muesebeck)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	0 1	0 2
G. nigrifemur Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 1 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1	0 2
G. pakmanus Gordh	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 0	0 1	0 2
G. philippinensis Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. punctaticeps (Kieffer)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 1 0	1 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. rutherfordi Krombein	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	1 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. sanctivicenti Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1	0 2
G. scitulus Evans	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1	0 2
G. silvestris (Evans)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 1	0 2
G. triangulus Kieffer	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. valvolicola Krombein	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 ? 0 ? ? 0	0 1	0 2
G. williamsi Bridwell	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 0	1 1	0 2
G. wirthi (Evans)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 0	1 2	0 2
Lytopsenella testaceicornis (Kieffer)	0 0 1 1 1 0 2 0 1	0 0 0 0 0 0 ? 1 0 1	0 0 1 1 1 1 0 1 1 1	0 0 0 0 0 1 0 1 0 1	0 0	0 4
Odontepyris bedus Alencar & Azevedo	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 0 0	2 0 1 1 1 ? 0 ? ? 0	0 1	0 2
O. fuscicrus (Kieffer)	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 1 0	2 0 1 1 1 2 0 ? ? 0	0 1	0 2
O. mandibularis Krombein	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 0 0	2 0 1 1 1 ? 0 ? ? 0	0 1	0 2
O. muesebecki Krombein	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 1 0	2 0 1 1 1 2 0 ? ? 0	0 1	0 2

Tab. 2. (*Continued*)

| Terminals | Characters | | |

Tab. 3. Morphological data matrix based on females constructed for the analyses; inapplicable, and unknown states are indicated as ?

| Terminals | Characters | | |

Tab. 3. (*Continued*)

Terminals	Characters 1	10	20	30	40	44
G. emigratus (Rohwer)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 1	1 0 0 0	0
G. floridanus (Ashmead)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. foveolatus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. fulvicornis (Rohwer)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. gelechiae Evans	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 1 ? 0 ? ? 1	1 0 0 0	0
G. hortorum Brues	0 1 1 1 1 0 1 0 0	1 0 0 0 0 0 0 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 1 ? 0 ? ? 1	1 0 0 0	0
G. hubbardi Howard	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. incompletus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	1 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. indicus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 0 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. jacintae Farrugia	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. longinervis Fouts	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. manilensis Kieffer	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. megacephalus Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. mellipes (Muesebeck)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 0 1 1 0	1 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. microstigmi Evans	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	1 0 1 1 0 0 0 ? ? 1	1 0 0 0	0
G. montanus (Motschulsky)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. natalensis Gordh	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 1 ? 0 ? ? 1	1 0 0 0	0
G. nephantidis (Muesebeck)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 1	1 0 0 0	0
G. nigrifemur Ashmead	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 1 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 0 0 ? ? 1	1 0 0 0	0
G. pakmanus Gordh	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. punctaticeps (Kieffer)	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 1 0	1 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. seminole Evans	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 0 0 0 1	0 0 0 1 1 1 1 1 0 0	1 0 1 1 1 ? 0 ? ? 1	1 0 0 0	0
G. spilogaster Evans	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	1 0 1 1 0 0 0 ? ? 1	1 0 0 0	0
G. stomopterycis Ram & Subba Rao	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 0 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. triangulifer Kieffer	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. valvolicola Krombein	0 1 1 1 1 0 1 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0
G. williamsi Bridwell	0 1 1 1 1 0 1 0 1	1 0 0 0 0 1 1 0 0 1	0 0 0 1 1 1 1 1 0 0	0 0 1 1 0 ? 0 ? ? 1	1 0 0 0	0

Tab. 3. (*Continued*)

Terminals	Characters 1	10	20	30	40	44
Lytopsenella herbsti (Kieffer)	0 1 1 1 1 0 2 0 1	0 0 0 0 0 0 ? 1 0 1	0 0 1 1 1 1 0 1 1 1	1 0 0 0 0 1 0 1 0 1	1 1 0 0	1
L. testaceicornis (Kieffer)	0 0 1 1 1 0 2 0 1	0 0 0 0 0 0 ? 1 0 1	0 0 1 1 1 1 0 1 1 1	0 0 0 0 0 1 0 1 0 1	1 1 0 0	1
Odontepyris formosicola Terayama	0 0 0 1 1 0 1 0 1	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 1	0
O. mandibularis Krombein	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 0 0	2 0 1 1 1 ? 0 ? ? 1	1 0 0 1	0
O. muesebecki Krombein	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 1 0	2 0 1 1 1 2 0 ? ? 1	1 0 0 1	0
O. quadrifoveatus (Muesebeck)	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 1	0
O. ruficrus Krombein	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 1 0	2 0 1 1 1 2 0 ? ? 1	1 0 0 1	0
O. ventralis Krombein	0 0 0 1 1 0 1 0 0	1 1 1 1 1 0 ? 1 1 0	1 0 0 1 1 1 0 0 0 0	2 0 1 1 1 ? 0 ? ? 1	1 0 0 1	0
Prosierola cubana Evans	0 0 1 1 1 0 1 1 1	1 1 0 1 1 1 0 0 1 0	0 1 0 1 1 1 0 1 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 0	1
P. flavicoxis (Kieffer)	0 0 1 1 1 0 1 1 1	1 1 0 1 1 1 0 0 1 0	0 1 0 1 1 1 0 1 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 0	1
P. nasalis (Westwood)	0 0 1 1 1 0 1 1 1	1 1 0 1 1 1 0 0 1 0	0 1 0 1 1 1 0 1 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 0	1
P. obliqua Evans	0 0 1 1 1 0 1 1 1	1 1 0 1 1 1 0 0 1 0	0 1 0 1 1 1 0 1 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 0	1
P. rufescens Evans	0 0 1 1 1 0 1 1 1	1 1 0 1 1 1 ? 0 1 0	0 1 0 1 1 1 0 1 1 0	2 0 1 1 1 0 0 ? ? 1	1 0 0 0	1
Sierola adamsoni Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. anthracina Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. antipoda Ashmead	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. armata Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. batrachedrae Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. blackburni Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. bryani Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. collaris Ashmead	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. comuana Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 ? 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. cookei Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 0 0 2 ? 1	1 0 0 1	0
S. depressa Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. distincta Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 ? 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. flavocollaris Ashmead	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. laticeps Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 ? 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. lebronnecii Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 ? 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. leeuwinensis Turner	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. megalognatha Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. monticola Cameron	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. nigrescens Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. oahuensis Ashmead	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. tahutaensis Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. tauraaiana Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. tenebriosa Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 ? 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0
S. vitiensis Fullaway	0 1 1 1 1 1 0 0 1	1 0 0 0 0 0 ? 0 0 1	0 0 0 1 1 1 0 1 1 0	0 1 1 0 0 2 0 2 ? 1	1 0 0 1	0

Appendix 1. Character coding for the present study (male species). Credits: P&K, characters used by Polaszek & Krombein (1994); T, characters used by Terayama (1995); P&N, characters used by De Ploëg & Nel (2004); *, new characters exclusively presented in this work.

Nº	Description
1*	Head, eye hairy: [0] absent; [1] present.
2 P&K, P&N	Head, presence of an unsculptured streak frontally: [0] present; [1] absent.
3*	Malar space, visibility in profile: [0] visible; [1] not visible.
4 P&K, T, P&N	Antenna, number of flagellomeres: [0] more than 12; [1] 11; [2] 10.
5*	Mandible, apical teeth count: [0] one; [1] three; [2] four.
6 P&K, T, P&N	Number of labial palp articles: [0] three; [1] two.
7 P&K, P&N	Number of maxillary palp articles: [0] four; [1] five; [2] six.
8 T, P&N	Pronotum, posterior margin: [0] almost straight; [1] slightly produced backward medially.
9*	Prosternum, size: [0] smaller than area of forecoxa; [1] At least large than area of forecoxa.
10 P&K, T, P&N	Mesoscutum, notaulus: [0] present; [1] absent.
11 P&K, P&N	Mesopleuron, gibbous in dorsal view: [0] absent; [1] present.
12 P&K, P&N	Mesopleuron, dentate process of mesopleuron in dorsal view: [0] absent; [1] present.
13 P&K, P&N	Mesoscutellum, mesoscutellar groove or pits: [0] present as fovea; [1] present as sulcus.
14*	Mesoscutellum, mesoscutellar fovea enlarged: [0] absent; [1] present.
15 P&K, P&N	Metapostnotum, triangular area marked dorsal smooth: [0] absent; [1] present.
16*	Metapostnotum, extension of triangular area: [0] up to the half propodeal disc length; [1] beyond the half propodeal disc length.
17 P&K, T, P&N	Metapostnotum, median metapostnotal carina: [0] absent; [1] present.
18 P&K, P&N	Metapectal-propodeal complex, metapostnotal-propodeal suture: [0] inconspicuous; [1] conspicuous.
19 P&K, T, P&N	Propodeum, posterior transverse carina of propodeal disc: [0] present; [1] absent.
20*	Propodeum, a pair of pits in basal outer portion of propodeum: [0] absent; [1] present.
21 P&K, T, P&N	Propodeum, a pair of conspicuous anterior pits on the propodeal disc: [0] absent; [1] present.
22 T, P&N	Legs, spine of metacoxae: [0] Simple, without a large blunt spine; [1] with a large blunt spine.
23*	Legs, number of tarsal claws: [0] one; [1] two.
24 T, P&N	Legs, strong curvature of tarsal claws: [0] absent; [1] present.
25 P&K, P&N	Petiole, ventral carina: [0] absent; [1] present.
26*	Petiole, shape of ventral carina: [0] straight; [1] bifurcated posterad.
27*	Forewing, bula: [0] absent; [1] present.
28*	Forewing, 2Cu vein: [0] absent; [1] present.
29*	Forewing, 1R1 vein: [0] well developed; [1] ill developed.
30 P&K, T, P&N	Forewing, length of 1Rs vein: [0] shorter than M vein; [1] as long as M vein; [2] longer than M vein.
31 P&K, P&N	Forewing, angle of distal margin of Rs vein: [0] without sharp angle; [1] with sharp angle.
32 P&K, T, P&N	Forewing, first radial cell (1R1): [0] present; [1] absent.
33 P&K, T, P&N	Forewing, second radial cell (2R1): [0] closed; [1] open.

34 P&K, T, P&N	Forewing, length of RS+M: [0] as long as or longer than 1Rs vein; [1] shorter than 1Rs vein.
35*	Forewing, shape of first medial cell (1M or areolet): [0] triangular; [1] pentagonal; [2] rectangular.
36 P&K, T, P&N	Forewing, length of second radial cell (2R1): [0] long; [1] short.
37*	Forewing, shape of second radial cell (2R1): [0] elliptical; [1] lanceolate; [2] triangular.
38*	Forewing, length of first radial cell (1R1): [0] shorter than second radial cell; [1] longer than second radial cell.
39*	Male genitalia, number of parameres: [0] one; [1] two.
40*	Male genitalia, ventral projection of apical lobe of aedeagus: [0] absent; [1] present.
41*	Male hypopygium, general shape: [0] triangular; [1] rectangular; [2] trapezoidal; [3] elliptical.
42*	Male hypopygium, degree of invagination of the posterior margin: [0] weak; [1] strong.
43*	Male hypopygium, shape of posterior margin: [0] bidentate; [1] straight; [2] medially bilobed; [3] medially convex; [4] medially concave; [5] totally/strongly concave; [6] totally/strongly convex.

Appendix 2. Character coding for the present study (female species). Credits: P&K, characters used by Polaszek & Krombein (1994); T, characters used by Terayama (1995); P&N, characters used by De Ploëg & Nel (2004); *, new characters exclusively presented in this work.

Nº	Description
1*	Head, eye hairy: [0] absent; [1] present.
2 P&K, P&N	Head, presence of an unsculptured streak frontally: [0] present; [1] absent.
3*	Malar space, visibility in profile: [0] visible; [1] not visible.
4 P&K, T, P&N	Antenna, number of flagellomeres: [0] more than 12; [1] 11; [2] 10.
5*	Mandible, apical teeth count: [0] one; [1] three; [2] four.
6 P&K, T, P&N	Number of labial palp articles: [0] three; [1] two.
7 P&K, P&N	Number of maxillary palp articles: [0] four; [1] five; [2] six.
8 T, P&N	Pronotum, posterior margin: [0] almost straight; [1] slightly produced backward medially.
9*	Prosternum, size: [0] smaller than area of forecoxa; [1] At least large than area of forecoxa.
10 P&K, T, P&N	Mesoscutum, notaulus: [0] present; [1] absent.
11 P&K, P&N	Mesopleuron, gibbous in dorsal view: [0] absent; [1] present.
12 P&K, P&N	Mesopleuron, dentate process of mesopleuron in dorsal view: [0] absent; [1] present.
13 P&K, P&N	Mesoscutellum, mesoscutellar groove or pits: [0] present as fovea; [1] present as sulcus.
14*	Mesoscutellum, mesoscutellar fovea enlarged: [0] absent; [1] present.
15 P&K, P&N	Metapostnotum, triangular area marked dorsal smooth: [0] absent; [1] present.
16*	Metapostnotum, extension of triangular area: [0] up to the half propodeal disc length; [1] beyond the half propodeal disc length.
17 P&K, T, P&N	Metapostnotum, median metapostnotal carina: [0] absent; [1] present.
18 P&K, P&N	Metapectal-propodeal complex, metapostnotal-propodeal suture: [0] inconspicuous; [1] conspicuous.

19	P&K, T, P&N	Propodeum, posterior transverse carina of propodeal disc: [0] present; [1] absent.
20*		Propodeum, a pair of pits in basal outer portion of propodeum: [0] absent; [1] present.
21	P&K, T, P&N	Propodeum, a pair of conspicuous anterior pits on the propodeal disc: [0] absent; [1] present.
22	T, P&N	Legs, spine of metacoxae: [0] Simple, without a large blunt spine; [1] with a large blunt spine.
23*		Legs, number of tarsal claws: [0] one; [1] two.
24	T, P&N	Legs, strong curvature of tarsal claws: [0] absent; [1] present.
25	P&K, P&N	Petiole, ventral carina: [0] absent; [1] present.
26*		Petiole, shape of ventral carina: [0] straight; [1] bifurcated posterad.
27*		Forewing, bula: [0] absent; [1] present.
28*		Forewing, 2Cu vein: [0] absent; [1] present.
29*		Forewing, 1R1 vein: [0] well developed; [1] ill developed.
30	P&K, T, P&N	Forewing, length of 1Rs vein: [0] shorter than M vein; [1] as long as M vein; [2] longer than M vein.
31	P&K, P&N	Forewing, angle of distal margin of Rs vein: [0] without sharp angle; [1] with sharp angle.
32	P&K, T, P&N	Forewing, first radial cell (1R1): [0] present; [1] absent.
33	P&K, T, P&N	Forewing, second radial cell (2R1): [0] closed; [1] open
34	P&K, T, P&N	Forewing, length of RS+M: [0] as long as or longer than 1Rs vein; [1] shorter than 1Rs vein.
35*		Forewing, shape of first medial cell (1M or areolet): [0] triangular; [1] pentagonal; [2] rectangular.
36	P&K, T, P&N	Forewing, length of second radial cell (2R1): [0] long; [1] short.
37*		Forewing, shape of second radial cell (2R1): [0] elliptical; [1] lanceolate; [2] triangular.
38*		Forewing, length of first radial cell (1R1): [0] shorter than second radial cell; [1] longer than second radial cell.
39*		Female genitalia, furcula V-shaped: [0] absent; [1] present.
40*		Female genitalia, proximal projection of the second valvifer (2vf): [0] absent; [1] present.
41*		Female genitalia, basal region of second rami valvularum (2rv) broadly enlarged: [0] absent; [1] present.
42*		Female genitalia, thickness of proximal projection of the second valvifer (2vf): [0] slender; [1] broadly enlarged.
43*		Female genitalia, proximal margin of first valvifer (1vf) angled: [0] absent; [1] present.
44*		Female genitalia, distal region of dorsal area of the Tergite 9 (T9) enlarged: [0] absent; [1] present.

CÁPITULO 4

CHAPTER 5 - SUBFAMILY BETHYLINAE HALIDAY, 1839

(Type-genus: *Bethylus* Latreille, 1802)

Subfamily Bethylinae Haliday, 1839

(Type-genus: *Bethylus* Latreille, 1802)

Bethylini: Kieffer, 1914d, 41: 507.

Bethylinae: Berland, 1928, 10: 99.

Diagnosis ♀ ♂

- Antenna with 10 or 11 flagellomeres
- Mandible thick, short, with four sharpened apical teeth
- Clypeus extending posterad into frons for short distance
- Clypeal carina strongly convex in profile
- Posterior pronotal margin convex medially
- Notauli absent or present
- Tarsal claws bifid and strongly angled
- RS+M vein tubular at least as a stub
- Hypopygium rectangular, triangular, and bilobate (♂)
- Second valvifer base with slender projection (fulcral arm) (♀)

Taxonomy. The genera of this subfamily are clearly different one from another; their taxonomic boundaries are well established, except for *Goniozus* Förster. Their sexual dimorphism is reduced so that it is easy to associate the sexes at least at genus rank.

The hypothesis that the subfamily Bethylinae is regarded as a sister-group of Pristocerinae + Epyrinae has been presented by Evans (1964), Mayhew and Hardy (1998) and Hardy and Mayhew (1998). According to Ramos & Azevedo (2016) seven of the eight living Bethylinae genera are monophyletic, except for *Goniozus*. In this cladistic analysis the polytomy involving *Eupsenella*, *Lytopsenella*, and remaining six genera was solved.

The main efforts both morphological and cladistically involving the genera of Bethylinae now should be focused in *Goniozus*. This genus is the second most in number of species in Bethylinae, with approximately 170 species. This genus is present worldwide, recorded from the Oriental, Neotropical, Nearctic, Palearctic, Afrotropical, and Australian regions. Due the several morphological patterns shown is clear the need of works whose main goal is to understand the genus more fully.

Moreover, Ramos et *al.* (2014) present a revision of Bethylinae fossils from Baltic, Rovno and Oise amber.

Genera included (11). *Afrobethylus* Ramos & Azevedo, 2016; *Bethylus* Latreille, 1802; *Cretobethylellus* Rasnitsyn, 1990 (fossil); *Eupsenella* Westwood, 1874; *Goniozus* Förster, 1856; *Lytopsenella* Kieffer, 1911; *Nucifrangibulum* Cockx, McKellar & Perrichot, 2016; *Odontepyris* Kieffer, 1904; *Omaloderus* Walker, 1843; *Prosierola* Kieffer, 1905; *Sierola* Cameron, 1881.

Species included (540). See the list genus by genus below.

Hosts. Mainly lepidopterous larvae

Key to the living genera of Bethylinae (males and females)

1. Antenna with 10 flagellomeres (Figs 18C; 19C).....2
1'. Antenna with 11 flagellomeres (Figs 21C; 21F; 23A)……..4
2. Eye hairy (Figs 20A–C); head large (Figs 19A; 20A–C); head always viper-shaped (Figs 25A; 25C)…….***Bethylus* (sensu *Anoxus*)**
2'. Eye glabrous (Figs 18A–B; 21A; 22A; 23A; 24A; 25A); head varying in length of medium to large (Figs 18A; 21A; 22A; 23A; 24A; 25A); head not always viper-shaped (Figs 20C; 21B; 21E; 22A; 24B; 25B)……3
3. Ventral carina of petiole present; female genitalia with proximal projection of the second valvifer (2vf) broadly enlarged (Figs),; 2R1 cell closed (Figs 18G–H) ……...***Afrobethylus***
3'. Ventral carina of petiole absent; female genitalia with proximal projection of the second valvifer (2vf) slender, and basal region of the second ramus of second valvifer not enlarged (Figs); 2R1 cell open (Fig 19F)…….***Bethylus* (*sensu strictu*)**
4. Pronotal disc not very short (Fig. 18F); Posterior pronotal margin convex medially (Fig. 24D)……..5
4'. Pronotal disc very short (Fig. 22D); Posterior pronotal margin not convex medially (Fig. 22D) ……***Nucifrangibulum***
5. Forewing with six closed cells (Figs 20G; 22B)……6

5’. Forewing with five or less closed cells (Figs 18G–H; 19F; 21J–K; 22B; 23G; 24G; 25H)……7

6. Forewing with 1R1 cell longer than or as long as 2R1 cell (Fig. 20G); forewing with 2R1 cell elliptical (Fig. 20G); notauli always present (Figs 20D–F)……***Eupsenella***

6’. Forewing with 1R1 cell shorter than 2R1 cell (Fig. 22B); 2R1 cell lanceolate (Fig. 22B); notauli usually absent (Fig. 22C)…….***Lytopsenella***

7. Metapectal-propodeal complex with metapostnotal propodeal suture (Figs 20D; 23C; 24E); mesopleuron prominent (Figs 23D; 24F)……...8

7’. Metapectal-propodeal complex without metapostnotal propodeal suture (Figs 19D; 24G–H); mesopleuron not prominent (Figs 19D; 24H)……..9

8. Metapectal-propodeal complex with pair of anterior pits (Figs 24D–F), and without pair of pits in basal outer portion (Figs 24D–F)…….***Prosierola***

8’. Metapectal-propodeal complex without pair of anterior pits (Figs 23D–E), and with pair of pits in basal outer portion (Figs 23C; 23E)……..***Odontepyris***

9. Forewing with 2R1 cell open (Figs 21–K); metapostnotum with basal triangle sculptured (Figs
21G)……..***Goniozus***

9’. Forewing with 2R1 cell closed (Figs 25H); metapostnotum with basal triangle indistinct (Figs
25G)……..***Sierola***

Afrobethylus Ramos & Azevedo, 2016

(Fig. 18 A–H)

Original description— Ramos & Azevedo 2016, 4097: 496.

Type species— *Afrobethylus zulu*, Ramos & Azevedo, 2016.

Kind of designation – original designation.

Designator— Ramos & Azevedo 2016, 4097: 496.

Diagnosis ♀ (♂ unknown)

- Palpal formula 5:2

- Antenna with 10 flagellomeres
- Notauli absent
- Parapsidal furrows present
- Metapectal-propodeal complex with metapostnotal median carina absent
- Prosternum large and diamond shaped
- 1M cell absent and 2R1 cell closed
- Ventral carina of petiole present and short
- Female genitalia with of proximal projection of the second valvifer (2vf) broadly enlarged
- Female genitalia with proximal margin of first valvifer angled

Taxonomy. *Afrobethylus* is similar to *Bethylus*, mainly due to the general habitus, the antenna with 10 flagellomeres, and the forewing without 1M cell. However, this genus also has some diagnostic characters of *Sierola*, such as the forewing with 2R1 cell closed, subtriangular, and long. Differently of *Bethylus* that have distribution Holarctic, and *Sierola* with distribution circum-pacific belt, *Afrobethylus* only can be founded in the Afrotropical region, and including Madagascar

Ramos & Azevedo (2016) proposed a hypothesis of relationship for the Bethylinae genera. This cladistic analysis recovered *Afrobethylus* as a monophyletic group, and sister-group of *Bethylus*.

Starting point. This genus was revised by Ramos & Azevedo (2016).

Distribution. Afrotropical region, 06 species.

Hosts. Unknown.

Check list

antankarana Ramos & Azevedo, 2016
antemoro Ramos & Azevedo, 2016
bapedi Ramos & Azevedo, 2016
swazi Ramos & Azevedo, 2016
vezo Ramos & Azevedo, 2016
zulu Ramos & Azevedo, 2016

Bethylus Latreille, 1802

(Fig. 19 A–G)

Original description— Latreille, 1802, 3: 315.

Type-species— *Omalus fuscicornis* Jurine, 1807.

Kind of designation— subsequent designation.

Designator— ICZN Opinion 153 in 1944.

Synonymous.

Anoxus Thomson, 1862. Synonymy by Polaszek & Krombein 1994, 3: 98.

Original description— Thomson 1862, 18: 452.

Type-species— *Anoxus boops* Thomson, 1862.

Kind of designation – original monotypy.

Designator— Thomson 1862 18: 452.

Anoxys Dalla Torre, 1898. Unjustified emendation to *Anoxus* by Dalla Torre (1898, 5: 550).

Perisemus Förster, 1856. Synonymy by Kieffer 1905 (in Kieffer & Marshall 1904–1906), 9: 243, 267.

Original description— Förster 1856, 2: 95–96.

Type-species— *Bethylus triareolatus* Förster, 1856.

Kind of designation— original designation.

Designator— Förster 1856, 2: 95–96.

Episemus Thompson, 1862. Synonymy by Richards 1939b, 89, 305.

Original description— Thompson 1862, 18: 452.

Type-species— *Episemus variabilis* Thomson, 1862.

Kind of designation— subsequent designation.

Designator— Richards 1939, 88: 305.

Digoniozus Kieffer, 1905. Synonymy by Evans 1962a, 150: 1.

Original description— Kieffer 1905 (in Kieffer and Marshall, 1904–1906), 9: 245.

Type-species— *Digoniozus* Kieffer, 1905.

Kind of designation— original monotypy.

Designator— Kieffer 1905 (in Kieffer and Marshall, 1904–1906), 9: 245.

Diagnosis ♀ ♂

- Palpal formula 5:2
- Body small to median-sized in both sexes
- Clypeus short, and not strongly angulated medially
- Antenna with 10 flagellomeres
- Notauli absent
- Parapsidal furrows present
- Mesoscutum short
- Metapectal-propodeal complex with lateral carina present
- Metapectal-propodeal complex with metapostnotal median carina absent
- Prosternum large, and diamond shaped
- Forewing without prostigma
- Hypopygium with posterior margin bilobate (♂)
- Parameres double, completely divided into dorsal and ventral arms (♂)
- Forewing of macropterous forms with:
    - Three closed cells (R, 1Cu, and C)
    - Rs vein forming almost right angle and giving rise to RS+M vein short as stub
    - 2R1 cell opened apically

Brachypterous forms:

- Tegula present

Micropterous forms:

- Mandible with three sharp apical teeth
- Forewing short, not reaching posterior margin of metapectal-propodeal complex
- Forewing oval

Taxonomy. *Bethylus* has fully winged forms, but there still are brachypterous or micropterous in a few species. Most of the species (both sexes) are polymorphic for wing length, and no fully winged North American species are known.

There are some specimens from African fauna, e.g. from Madagascar, and South Africa, very similar to *Bethylus*, namely: *Afrobethylus*. However, such species present striking differences in relationship to *Bethylus*, such as the 2R1 cell closed, the ventral carina of petiole present, the female genitalia with basal region of the second ramus of second valvifer broadly enlarged, the proximal projection starting from base of second valvula, and the proximal margin of the 1vf angled.

On the other hand, the genus *Anoxus* was synonymized with *Bethylus* by Polaszek and Krombein (1994) due their similarity with *Bethylus*. According to these authors the only difference found between these two genera is the eyes are setose or not, and other characters are identical in the two genera. Based on this scenario, Polaszek and Krombein (1994) mentioned this character as varying intra generically. Therefore, they proposed *Anoxus* as junior synonym of *Bethylus*.

Finally, there is no denying the similarity between *Anoxus*, and *Bethylus*. But, based on our observations is clear, at least, two clear patterns of variation in *Bethylus*. Furthermore, one of this patterns represent the old concept of *Anoxus*, mentioned here as "*Anoxus style"* (see more details in the key to the living genera of Bethylinae).

Starting point. This genus was treated in some detail by Richards (1939) and Evans (1964).

Distribution. Holarctic, 37 species.

Hosts. Parasitoid of small lepidopterous larvae (Evans 1964, Richards 1939). There are reports of *B. cephalotes* attacking larvae of Agonoxenidae, Tortricidae, Zygaenidae (Richards 1939), *B. dendrophilus* attacking larvae of Cosmopterigidae (Richards 1939), and *B. fuscicornis* from Coleophoridae and Gelechiidae (Richards 1939); *B. decipiens* was founded attacking *Cnephasia larva* (Tortricidae) (Evans 1964); *B. ameonus* attacking the olethreutid moth *Rhopobata naevana* and the nitidulid beetle *Brachypterolus pullicarius* (Richards 1939).

Check list

amoenus Fouts, 1928
amplipennis (Motschulsky, 1863)
apteryx Kieffer, 1905
arcuatus Kieffer, 1905

boops (Thompson, 1861)
cenopterus (Panzer, 1801)
cephalotes (Förster, 1860)
coniceps (Kieffer, 1904)
decipiens (Provancher, 1887)
dendrophilus Richards, 1939
dubius (Kieffer, 1904)
formicarius (Panzer, 1806)
fuscicornis (Jurine, 1807)
fuscipennis Klug, 1810
gaullei Kieffer, 1905
gestroi (Kieffer, 1904)
hamatus Kieffer, 1905
hemipterus (Panzer, 1801)
himalayanus Terayama, 2004
hyalinus (Marshall, 1874)
latus Wollaston, 1858
linearis Wollaston, 1858
lineatus Kieffer, 1905
mandibularis (Kieffer, 1904)
musculus Say, 1836
nitidus (Thomson, 1862)
nudipennis Klug, 1810
paradoxis Nagy, 1970
pilosus (Kieffer, 1904)
punctatus Latreille, 1804
ruficornis Klug, 1810
rufipes (Kieffer, 1904)
sarobetsuensis Terayama, 2006
shigaensis Terayama, 2006
sinensis Xu, He & Terayama, 2002
struvei Szelenyi, 1941
tenuis Wollaston, 1858

Cretobethylellus Rasnitsyn, 1990

Original description— Rasnitsyn 1990, 200.

Type-species— *Cretobethylellus lucidus* Rasnitsyn, 1990.

Kind of designation— original monotypy.

Designator— Rasnitsyn 1990, 200.

Diagnosis (?sex)

- Head subquadrate in dorsal view, and apparently flat
- Antennal scape relatively long
- Frons with longitudinal sulcus transpassing anterior ocellus
- Eye large
- Ocellar triangle entirely below to imaginary line of top eye, far from vertex crest, close to eye, its front angle clearly obtuse
- Malar space conspicuous
- Gena large, intergenal suture conspicuous
- Mesosoma very wide, wider than head
- Pronotal disc with anterior margin strongly convex and posterior margin somewhat angled forward
- Mesoscutum about as long and mesoscutellum
- Notauli well-impressed, almost straight, slightly convergent posteriorly
- Metapectal-propodeal complex short
- Propodeal declivity with slope abruptly declivous
- Forewing with three closed cells (C, R, 1Cu), 2Cu well-defined and apparently closed
- RS+M vein tubular, well-pigmented, short, straight, and subparallel to wing posterior margin
- Rs&M slightly angled medially

Taxonomy. According to Rasnitsyn (1990) this genus is similar to *Bethylus*, and its morphological ground plan similar to Bethylinae. He described the metapectal-propodeal complex as strongly areolate, but we were not able without observing directly the specimen.

This genus can be considered as Bethylinae because the forewing has the RS+M and Rs&M of forewing slightly angled medially.

Starting point. This genus was treated in some detail by Rasnitsyn (1990), with some illustrations.

Distribution. Late Mesozoic Transbaikalia (Russia, Pavlovka), 01 species.

Hosts. Unknown.

Check list

lucidus Rasnitsyn, 1990

Eupsenella Westwood, 1874

(Fig. 20 A–H)

Original description— Westwood 1874, 168.

Type-species— *Eupsenella agilis* Westwood, 1874.

Kind of designation— original monotypy.

Designator— Westwood 1874, 168.

Synonymous.

Protobethylus De Ploëg & Nel, 2004. Synonymy by Ramos *et al.* 2014, 271: 205–206, 209.

Original description— De Ploëg & Nel 2004, 2: 75–82.

Type-species— *Protobethylus eocenicus* De Ploëg & Nel, 2004.

Kind of designation— original monotypy.

Designator— De Ploëg & Nel 2004, 2: 75–82.

Fushunochrysites Hong, 2002 **Syn. nov.**

Original description— Hong 2002, 2: 314–315.

Type-species— *Fushunochrysites eocenicus* Hong, 2002.

Kind of designation— original monotypy.

Designator— Hong 2002, 2: 314.

Diagnosis ♀ ♂

- Palpal formula 6:3
- Mandible with four sharpened apical teeth
- Median clypeal lobe truncate, angulate or subangulate
- Median carina of clypeus present or absent
- Lateral lobe of clypeus almost absent
- Hypostomal carina well defined
- Notauli present
- Notauli well defined
- Metapectal-propodeal complex with metapostnotal median carina and without transverse posterior carina
- Prosternum diamond shaped, large, 0.7–1.0 x area of procoxa, excavated medially
- Forewing with prostigma ill-defined
- Ventral carina of metasomal petiole straight
- Hypopygium with posterior margin bidentate and angulate (♂)
- Paramere simple or double (♂)

Macropterous forms (♀ ♂):

- Forewing with six closed cells (R, 1Cu, C, 1M, 1R1 and 2R1)
- 2R1 cell short
- Hind wing with incipient A_3v and jugal lobe

Brachypterous forms (♀):

- 1M cell present or absent
- 1R1 cell in the forewing present or absent
- 2R1 cell in the forewing opened
- Forewing with pterostigma subtriangular
- Tegula present

Taxonomy. The most distinctive feature of *Eupsenella* is the forewing with six closed cells, being the 2R1, 1R1 and 1M cells closed. *Lytopsenella* Kieffer is the only genus in Bethylidae

with this condition. However in *Eupsenella* the 2R1 cell is short, slightly higher than 1R1 cell, whereas in *Lytopsenella* it is elongate (Ramos & Azevedo 2012). The comparatively large number of closed cells is regarded as primitive because most bethylids have fewer closed cells in the forewing.

The fossil family Fushunochrysidae proposed by Hong (2002) was synonymized with Bethylidae Haliday, 1839 based on their morphological similarity. The single genus of this family is *Fushunochrysites* Hong, 2002 and its single species *F. eocenicus* Hong, 2002 was established as its type-species. Here we propose that the best placement of this monotypic genus in Bethylidae is into Bethylinae. *Fushunochrysites* displays on its forewing several characters that are also present in all members of *Eupsenella* (see more details in Ramos & Azevedo 2012, pg. 62, and Ramos *et al.* 2014), because both genera have the forewing with six closed cells (R, 1Cu, C, 1M, 1R1 and 2R1), and the 2R1 cell short. Thus, considering these evidences, we are propose here *Fushunochrysites* as a new junior synonym of *Eupsenella* and transfer *F. eocenicus* Hong, 2002 to *Eupsenella*.

Sinibethylus from Chinese Xilutian coal mine, Eocene terrestrial Fushun amber, is here also synonymized with *Eupsenella*, because of its general habitus, and characters of mandible and forewing. Thus here propose *Sinibethylus* as a new junior synonym of *Eupsenella* and transfer its single species *S. eocenicus* Hong, 2002 to *Eupsenella*.

Starting point. Ramos & Azevedo (2012) presented a revision of the genus including key, diagnosis and illustrations of its species.

Distribution. Australian region, 45 species. Baltic, Chinese, Rovno and Oise ambers, 07 species.

Hosts. *Eupsenella* parasitizes lepidopterous larvae (Riek 1970) and leafroller lepidopterous larvae (Berry 1998; Gordh & Harris 1996). Recent fieldwork conclusively identifies the host for *E. insulana* as the tortricids *Harmologa amplexana* (Zeller) and *Planotortrix octo* Dugdale recovered from the nest of the eumenid *Ancistrocerus gazella* (Panzer) (Gordh & Harris 1996). These authors also indicated a female *E. insulana* was taken attacking the tortricid *Eurythecta zelaea* Meyrick in *Colobanthus brevisepalus* Kirk. According to Berry (1998) all tortricids species parasitized by *E. insulana* are native from New Zealand. The discovery of hosts for *Eupsenella* (*E. insulana*) is noteworthy and consistent with the host records of most

other Bethylinae which attack moth larvae (Gordh & Harris 1996). Moreover, Paul and Austin (2006) indicated that *Eupsenella* parasitizes the tortricids *Epiphyas postvittana* (Walker). According these authors this tortricid is a serious pest of a number of horticultural crops including grapes in Australia and New Zealand.

Check list

agilis Westwood, 1874
ajabatha Ramos & Azevedo, 2012
alawa Ramos & Azevedo, 2012
alura Ramos & Azevedo, 2012
antakirinja Ramos & Azevedo, 2012
araba Ramos & Azevedo, 2012
arabana Ramos & Azevedo, 2012
aulax Ramos & Azevedo, 2014
baada Ramos & Azevedo, 2012
barada Ramos & Azevedo, 2012
barna Ramos & Azevedo, 2012
batjala Ramos & Azevedo, 2012
bilingara Ramos & Azevedo, 2012
bubumara Ramos & Azevedo, 2012
ceciliae Terayama, 2004
dalla Ramos & Azevedo, 2012
diemenensis Dodd, 1916
djagaraga Ramos & Azevedo, 2012
eocenica (De Ploëg & Nel, 2004)
eora Ramos & Azevedo, 2012
flavifemorata Terayama, 2004
fuscipennis Cameron, 1888
ilba Ramos & Azevedo, 2012
inawonga Ramos & Azevedo, 2012
inggarda Ramos & Azevedo, 2012
ingura Ramos & Azevedo, 2012
insulana Gordh & Harris, 1996

iwaidja Ramos & Azevedo, 2012

jaadwa Ramos & Azevedo, 2012

jaara Ramos & Azevedo, 2012

jaburara Ramos & Azevedo, 2012

jadira Ramos & Azevedo, 2012

jagara Ramos & Azevedo, 2012

janda Ramos & Azevedo, 2012

kabalbara Ramos & Azevedo, 2012

kaibara Ramos & Azevedo, 2012

karanja Ramos & Azevedo, 2012

karawa Ramos & Azevedo, 2012

klesoviana Ramos & Azevedo, 2014

kokatha Ramos & Azevedo, 2012

larrakia Ramos & Azevedo, 2012

malgana Ramos & Azevedo, 2012

maya Ramos & Azevedo, 2012

nagatara Ramos & Azevedo, 2012

nanda Ramos & Azevedo, 2012

neoeocenica Ramos & Azevedo **nom. nov.** from *Fushunochrysites*

pangkala Ramos & Azevedo, 2012

proxima Kieffer, 1911

reticulata Terayama, 2004

rossica Ramos & Azevedo, 2014

wanamara Ramos & Azevedo, 2012

yantarnica Ramos & Azevedo, 2014

Goniozus Förster, 1856

(Fig. 21 A–K)

Original description— Förster 1856, 2: 95–96.

Type-species— *Bethylus claripennis* Förster, 1851.

Kind of designation— subsequent designation

Designator— Ashmead 1893, 45: 72.

Synonymous.

Parasierola Cameron, 1883. Synonymy by Evans 1978b, 27: 225–226.

Original description— Cameron 1883, 197.

Type-species— *Parasierola testaceicornis* Cameron, 1883.

Kind of designation— original monotypy

Designator— Cameron 1883, 197.

Progoniozus Kieffer, 1905. Synonymy by Evans 1978b, 27: 226.

Original description – Kieffer 1905a, 29: 105.

Type-species— *Perisemus f1oridanus* Ashmead, 1905.

Kind of designation— original designation.

Designator— Kieffer 1905a, 29: 105.

Perisierola Kieffer, 1914. Synonymy by Evans 1978b, 27: 226.

Original description— Kieffer 1914d, 41: 533.

Type-species— *Parasierola gallicola* Kieffer 1905.

Kind of designation— subsequent designation.

Designator— Muesebeck & Walkley 1951, 2: 733.

Messoria Meunier, 1916. **Syn. nov.**

Original description— Meunier 1916, 68: 392–393.

Type-species— *Messoria copalina* Meunier, 1916.

Kind of designation— original monotypy.

Designator— Meunier 1916, 68: 392–393.

Diagnosis ♀ ♂

- Palpal formula 5:3
- Clypeus anteriorly with strongly produced angular or subangular median lobe
- Eye large, with or without erect hairs
- Notauli absent

- Mesoscutellum with transverse basal groove or pair of small pits connected by weak groove
- Metapectal-propodeal complex with transverse posterior carina absent, complete or incomplete, and without metapostnotal median carina
- Forewing with:
  - Prostigma large and triangular
  - Pterostigma large
  - 2R1 cell open
  - 1M cell present (areolet) or present only RS+M vein
  - Rs vein curved and not forming angle

Taxonomy. *Goniozus* is worldwide in distribution, and is the second genus in number of species of Bethylinae. Undoubtedly it is the genus with the highest degree of taxonomic confusion regarding its boundaries. The species of *Goniozus* are apparently somewhat variable and not always easily distinguished. Thus, establishing patterns for this genus is a task extremely complex. Evans (1978b) proposed the synonymy of *Parasierola* and *Perisierola* under *Goniozus*. The main pattern observed in *Goniozus* after this proposition refers to the first medial cell closed in the species coming from *Parasierola* and the first medial cell opened in the species coming from *Goniozus s.str.*.

Evans (1978b) presented the first attempt to revise this large and difficult genus, but he was sure that your attempt does not would be the last word on the subject. Evans (1978b) divided the genus into a series of nine species-groups. Some groups of "*Parasierola*", especially the *mexicanus* group, appear more similar to certain groups of *Goniozus s.str*. (in this case the *megacephalus* group) than to other groups of "*Parasierola*". In practice, the differences between these species-groups are in most cases ill-marked, and also within each group the separation of the species is often difficult.

Herein, the fossil genus *Messoria* from Pleistocene copal of Zanzibar was synonymized with the living genus *Goniozus* based on its similarity with the Bethylinae species. *Messoria* was described originally by Meunier (1916), and such author provided description and illustrations of *Messoria*. This genus is characterized by having antennae with 11 flagellomeres, the metathorax convex, the metasoma oval, the legs strong, the metatarsus cylindrical in shape, the metatarsus I longer than II-V together, and the forewing with RS+M present and long.

Gordh & Móczár (1990) included *Messoria* in Epyrinae without any explanation. Perrichot & Nel (2008) corroborated the proposition of Gordh & Móczár based in general body pattern of this species. Moreover, they mentioned that *Messoria* differs from *Rhabdepyris gallicus* by its more developed forewing venation with RS+M present and long. We were not able of observing directly the specimen. However, based on photographs of the type-species of *Messoria*, and their description, we can understood that all features presented for *Messoria* can be easily addressed into Bethylinae. Thus we disagree of the proposal of Gordh & Móczár (1990) and Perrichot and Nel (2008) that included *Messoria* in Epyrinae, mainly based on the forewing, RS+M present and long, one of the diagnostic features of *Goniozus*, so that we here propose *Messoria* as a new junior synonym of *Goniozus* and transfer its single *Messoria copalina* Meunier, 1916 to *Goniozus*.

Starting point. Evans (1978b) presented a review of the genus from Nearctic region including key, and the proposition of *Goniozus* into a series of nine species-groups. Terayama (2006) presented a revision of the genus from Sino-Japanese region including key, diagnosis and illustrations of its species. A world revision is still missing.

Distribution. Cosmopolitan, 174 species.

Hosts. Gordh & Móczár (1990) listed 140 nominal species of this genus and all of them are presumed to be primary external parasitoids of lepidopterous larvae. Members of this genus are a cosmopolitan with the potential of being a biological control agent against various lepidopterous pests (Gordh and Witethom, 1995). For instance, *Goniozus legneri* Gordh is commercially using as a biological control agent against for Navel Orange Worm, *Amyelois transitella* Walker (Lepidoptera: Phycitidae) (Sterling Insectary, 2011).

Santhosh & Narendran (2009) described the first bethylid species reared from *Helicoverpa armigera*. Vadivelu *et al.* (1975) and Divakar et *al.* (1983) reported two undescribed species of *Goniozus* as larval parasitoids of *Helicoverpa armigera* (Hübner) from south India. However, according to Santhosh and Narendran (2009) the voucher specimens of these reports are lost and have not been available for study.

Goniozus jacintae Farrugia was introduced into New Zealand in the late 1960s as a biological control agent for the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera, Tortricidae). Based on this scenario, Berry (1998) indicated *G. jacintae* as fairly

widely in New Zealand. According this author, *G. jacintae* parasite the native tortricids *Ctenopseustis obliquana* (Walker), *Planotortrix notophae* (Turner), and *Epiphyas postvittana* (Walker). However, other Lepidoptera species were recorded from New Zealand by Ward (2013) including *Epalxiphora axenana* Meyrick, *Planotortrix excessana* (Walker), *Planotortrix octo* Dugdale and *Prays nephelomima* Meyrick. *G. jacintae* also was found parasitizing *E. postvittana* in Australia. Moreover, other *Goniozus* species was found parasitizing this tortricid, namely: *G. mandibulatus* (see more details in Paul & Austin 2006, pg. 153).

Although most members of *Goniozus* have been recorded as ectoparasitoid of immature stages of microlepidopterous families (e.g. Gelechiidae, Pyralidae, and Tortricidae) (Gordh & Móczár, 1990), one species, *G. microstigmi* Melo & Evans was recorded as parasite of Crabronidae (Melo and Evans 1993).

Santhosh & Ranjith (2015) presented a discussion on the association of *Goniozus* with insect induced plant galls. One of the most important issues on *Goniozus* is that *G. inauditus* Santhosh and Ranjith was reared from *Crotonothrips* sp. induced leaf galls of *Memecylon umbellatum* and this species also can be found associated with *Carpelimus* sp. as gall inhabitants. Moreover, *G. kuriani* Santhosh & Ranjith emerged from the leaf galls induced by *Trioza jambolanae* Crawford (Hemiptera: Triozidae) (see more details in Santhosh and Ranjith 2015).

Check list

aethiops Evans, 1976
ahmeadi Kurian, 1955
akitsushimanus Terayama, 2006
alayoellus Evans, 1970
angulatus (Muesebeck, 1933)
antileanus Evans, 1969
antipodum Westwood, 1874
arcuatus (Kieffer, 1911)
armigerae Santhosh & Narendran, 2009
asperulus Evans, 1978
baishanzuensis Xu, He & Terayama, 2002
bogotensis (Kieffer, 1909)

boliviensis (Kieffer, 1910)
borneanus Cameron, 1910
breviceps (Krombein, 1954)
brevicornis Kieffer, 1904
brevinervis Fouts, 1928
cariborum Evans, 1969
carinatus Kieffer, 1905
castaneicolor Evans, 1964
castaneus Kieffer, 1905
cellularis (Say, 1836)
chatterjii Kurian, 1955
chowdhari Kurian, 1955
ciliatus (Evans, 1970)
clarimontis Kieffer, 1906
claripennis (Förster, 1851)
clarkei Evans, 1969
collessi Farrugia, 1981
comatus Krombein, 1996
complanatus Evans, 1978
contractus (Brues, 1933)
copalinus (Meunier, 1916) **comb. nov.** from *Messoria*
crassifemur Evans, 1969
cristatus Evans, 1969
cuttockensis Lal, 1939
definitus Ramos & Azevedo, 2014
delhiensis Ram, 1969
depressus Kieffer, 1913
disjunctus (Kieffer, 1926)
ecarinatus Krombein, 1996
electus Fouts, 1928
emigratus (Rohwer, 1917)
eriae Terayama, 2006
etielae Risbec, 1955

excisus (Kieffer, 1909)
flavipes Fouts, 1928
floridanus (Ashmead, 1887)
foveolatus Ashmead, 1887
fratellus Evans, 1978
fulgidus Krombein, 1996
fulvicornis (Rohwer, 1915)
fuscicornis (Kieffer, 1908)
gallicola (Kieffer, 1905)
garouae (Risbec, 1955)
gelechiae Evans, 1978
gestroi Kieffer, 1904
giraulti Dodd, 1916
glabriscutellum Dodd, 1916
gordhi Evans, 1978
gracilicornis (Kieffer, 1906)
grandiceps (Kieffer, 1907)
hanoiensis Gordh, 1993
hoorai Terayama, 1999
hortorum Brues, 1907
hualienensis Terayama, 2004
hubbardi Howard, 1885
hybleae Kurian, 1955
hypsipylae Kurian, 1955
inauditus Santhosh, 2015
incompletus Ashmead, 1894
indicus Ashmead, 1903
indigens Evans, 1978
integrus (Kieffer, 1910)
iyonus Terayama, 2006
jacintae Farrugia, 1981
jamiei Ward, 2013
japonicus Ashmead, 1904

kabisus Benoit, 1957
kaiensis Terayama, 2006
keralensis Gordh, 1985
kiefferi (Gordh, 1986)
koreanus Lim, 2012
kuriani Santhosh, 2015
kusigematii Terayama, 1999
lamprosemae Xu, He & Terayama, 2002
layouanus (Evans, 1969)
legneri Gordh, 1982
leuconeurus (Kieffer, 1914)
leviceps (Kieffer, 1905)
longiceps Kieffer, 1904
longinervis Fouts, 1928
lucidulus Krombein, 1996
luteipes (Kieffer, 1907)
lygropiae Kurian, 1955
macrassippattanami Kurian, 1955
macrophthalma Kieffer, 1906
maculicornis (Ogloblin, 1954)
mandibulatus Farrugia, 1981
manilensis Kieffer, 1922
marasmi Kurian, 1955
marianensis Terayama, 1994
maurus Marshall, 1905
megacephalus Ashmead, 1893
mellipes (Muesebeck, 1934)
mesolevis Lim, 2012
mexicanus Ashmead, 1895
microstigmi Evans, 1993
mobilis Förster, 1860
montanus (Motschulsky, 1863)
mori Kurian, 1955

morindae Kurian, 1952
musae Ward, 2013
natalensis Gordh, 1986
nephantidis (Muesebeck, 1934)
nephoterycis Kurian, 1952
nigricoxis (Kieffer, 1904)
nigrifemur Ashmead, 1894
nilamburensis Kurian, 1955
occipitalis Kieffer, 1906
opacus (Cameron, 1888)
orbitalis Evans, 1978
pakmanus Gordh, 1984
palliditarsis (Cameron, 1888)
peruvianus (Kieffer, 1910)
philippinensis Ashmead, 1904
plugarui Nagy, 1976
politus Ashmead, 1893
procerae Risbec, 1956
prolixus Evans, 1978
pulveriae (Kurian, 1954)
punctaticeps (Kieffer, 1906)
punctatus (Kieffer, 1905)
raptor Evans, 1978
reclusus Evans, 1978
respectus Sorg, 1988
rivularis (Evans, 1969)
rostratus Kieffer, 1905
rugosus Samad, 1973
rutherfordi Krombein, 1996
rutshurus (Benoit, 1957)
ryukyuensis Terayama, 1999
salvadorae (Kurian, 1954)
sanctijohannis Kurian, 1955

sanctivincenti Ashmead, 1894
santaeclarae (Ogloblin, 1954)
scitulus Evans, 1978
seminole Evans, 1978
sensorius Gordh, 1988
silvestris (Evans, 1969)
similis Fouts, 1934
sinicus Xiao & Wu, 1987
spilogaster Evans, 1970
stomopterycis Ram & Subba Rao, 1967
swirskiana (Argaman, 1992)
tepicensis Ashmead, 1895
testacicornis (Cameron, 1883)
thailandensis Gordh & Witehom, 1995
thalasodes Kurian, 1955
tibialis Vollenhoven, 1878
timberlakei Evans, 1978
tosaensis Terayama, 1999
triangulifer Kieffer, 1914
triangulus Kieffer, 1922
ussuricus (Gorbatovsky, 1995)
valvolicola Krombein, 1996
villosus Krombein, 1996
virginalis Evans, 1970
williamsi Bridwell, 1919
wirthi (Evans, 1969)
xiaoi Xu, He & Terayama, 2002
yaeyamanus Terayama, 1999
yezo Terayama, 2006
yoshikawai Terayama, 2006

Lytopsenella Kieffer, 1911

(Fig. 22 A–D)

Original description— Kieffer 1911b, 35: 203.

Type-species— *Eupsenella herbsti* Kieffer, 1904.

Kind of designation— original monotypy.

Designator— Kieffer 1911b, 35: 203.

Diagnosis ♀ ♂

- Palpal formula 6:3
- Clypeus with median lobe large
- Median carina of clypeus continues to frons
- Notauli present
- Parapsidal furrows present
- Mesopleuron not prominent
- Metapectal-propodeal complex without transverse posterior carina
- Forewing with:
  - Six closed cells (R, 1Cu, C, 1M, 1R1 and 2R1)
  - 2R1 cell elongate
  - 2R1 cell distinctly longer than wide
  - Prostigma ill-defined
  - Pterostigma almost present
- Metasoma never petiolate
- Parameres double (♂)

Taxonomy. The genus is easily recognized within Bethylinae, because all members have the marginal cell in the forewing closed and elongate. *Lytopsenella* closely resembles *Eupsenella*, mainly differing in having the 2R1 cell clearly longer. In *Lytopsenella,* the 1R1 cell of the forewing is always significantly shorter than the 2R1 cell, whereas in *Eupsenella,* the 1R1 cell is equal to or longer than the 2R1 cell.

Starting point. Azevedo (2009b) presented a synopsis of the genus including key, diagnosis and illustrations of its species. Brues (1923), Ohl (1995) and Ramos *et al.* (2014) described six fossil species.

Distribution. Neotropical region, 02 species. Baltic amber, 06 species.

Hosts. Evans (1964) reported that there is a specimen of *L. herbsti* (Kieffer, 1904) deposited at Museum of Comparative Zoology labeled as having been taken while attacking an adult cantharid beetle.

Check list

baltica Ramos & Azevedo, 2014
crastina (Brues, 1923)
herbsti (Kieffer, 1904)
kerneggeri Ohl, 1995
maritima Ramos & Azevedo, 2014
setigera (Brues, 1923)
simplex (Brues, 1923)
testaceicornis (Kieffer, 1910)

Nucifrangibulum Cockx, McKellar & Perrichot, 2016

Original description— Cockx, McKellar & Perrichot, 2016, 68: 4-5
Type-species— *Nucifrangibulum carentonensis* Cockx, McKellar & Perrichot, 2016
Kind of designation— original monotypy.
Designator— Cockx, McKellar & Perrichot, 2016, 68: 4-5

Synonymous. None

Diagnosis ♀

- Head prognathous
- Mandible broad and bearing four apical teeth
- Clypeus rounded
- Ocelli at rear of head
- Pronotal disc very short
- Posterior pronotal margin not convex medially
- Metanotum with single row of foveae
- Metapostnotum sculptured dorsally.

Taxonomy. The main characters that support placement *Nucifrangibulum* within Bethylinae include the rounded clypeus with a fine carina continuing dorsally, and the absence of occipital carina. Moreover, the genus has a metapostnotum large, with ornamentation areolate-rugose type and metapectal-propodeal complex without metapostnotal median carina. The type species *Nucifrangibulum carentonensis* is partial: most of the antennae are missing as well as the wings, and the metasoma is torn. Thus, according to Cockx, et *al.* (2016) the new taxon cannot be assigned to any of the genera previously described.

Starting point. This genus was treated in some detail by Cockx, McKellar & Perrichot (2016).

Distribution. Charentese Amber, Fouras (IGR collection) (Cretaceous of France).

Hosts. Unknown.

Check list

carentonensis Cockx, McKellar & Perrichot, 2016

Odontepyris Kieffer, 1904

(Fig. 23 A–H)

Original description— Kieffer 1904a, 1: 378.

Type-species— *Goniozus transvaalensis* Buysson, 1897.

Kind of designation— original monotypy.

Designator— Kieffer 1904, 1: 378.

Synonymous.

Trissomalus Kieffer, 1905. Synonymy by Polaszek & Krombein 1994, 3: 98.

Original description— Kieffer 1905a, 29: 105.

Type-species— *Goniozus transvaalensis* Buysson, 1897.

Kind of designation— original monotypy.

Designator— Kieffer 1905a, 29: 105.

Diagnosis ♀♂

- Palpal formula 5:3
- Median lobe of clypeus large
- Median lobe of clypeus triangular or subtriangular
- Median carina of clypeus continues on well up the frons
- Notauli absent
- Mesopleuron large
- Mesopleuron bearing a dentate process in some species
- Metapectal-propodeal complex with metapostnotal median carina present
- Transverse carina of metapectal-propodeal complex present
- Metapectal-propodeal complex with pair of anterior pits
- Forewing with:
  - Prostigma present
  - Pterostigma very large
  - 2R1 cell open apically
  - 1M cell present (areolet)
  - RS+M shorter than Rs vein
- Ventral carina of petiole complete

Taxonomy. *Odontepyris* is one of the easiest recognizable genera of Bethylinae mainly due to the large size, and by having the dentate processes on the mesopleuron, the presence of median longitudinal, discal and transverse carina in the metapectal-propodeal complex. Polaszek and Krombein (1994) presented the mesopleuron moderately large as a synapomorphy of *Odontepyris* and *Prosierola* Kieffer. This condition was found also by De Ploëg & Nel (2004).

Starting point. Terayama (2006) presented a revision of the genus from Sino-japanese region (sensu Holt *et al.* 2013) including key, diagnosis and illustrations of its species. Lim *et al.* (2009) presented a revision of the genus from Oriental region including key, diagnosis and illustrations of its species and notes of species of the *Odontepyris* wasps founded laying eggs on the larva of *Telorta divergens* (Butler). Alencar and Azevedo (2011b) presented a revision of the genus from Madagascar including key, diagnosis and illustrations of its species.

Distribution. Old World (mainly Oriental) and Australian, 42 species.

Hosts. *Odontepyris* is ectoparasitoid of lepidopterous larvae: *O. argyriae* Kurian on *Argyria sticticraspis* Hamson (Pyralidae), *O. hypsipylae* (Kurian) on *Hypsipyla robusta* (Moore) (Pyralidae), *O. cirphi* Kurian on *Leucania* sp. (Noctuidae), *O. indicus* (Kurian) on *Diatraea saccharalis* (Fabricius) (Kurian 1954a; 1955); *O. mandibularis* Muesebeck on *Mythimna* sp. (Noctuidae), and *O. erucarus* (Szelényi) on *Epicallima formosella* (Denis & Schiffermüller) (Oecophoridae) (Georgiev *et al.* 2001); *Odontepyris telortis* Lim, Shin & Lee on *Telorta divergens* (Butler) (Lim *et al.* 2009).

Check list

acrius Alencar & Azevedo, 2011
acutus Lim, 2013
argyriae Kurian, 1954
batrae Kurian, 1955
bedus Alencar & Azevedo, 2011
cameroni (Kieffer, 1914)
cardamomensis Lim, 2013
cirphi Kurian, 1955
concavus Lim, 2013

cynpus Alencar & Azevedo, 2011

erucarus (Szelenyi, 1958) **comb. nov**. from *Goniozus*

escus Alencar & Azevedo, 2011

flavinervis Kieffer, 1904

formosicola Terayama, 1997

fudoh Terayama, 2006

fujianus Xu, He & Terayama, 2002

fuscicrus (Kieffer, 1907)

hainanus Xiao & Zu, 2008

hypsipylae (Kurian, 1955)

indicus (Kurian, 1954)

japonicus Terayama, 2006

koreanus Terayama, 1997

liukueiensis Terayama, 1997

mandibularis Krombein, 1996

marishi Terayama, 1999

moldavica (Nagy, 1976)

muesebecki Krombein, 1996

obtusus Zu & He, 2006

orientalis Gorbatovsky, 1995

ovatus Xu & He, 2006

peringueyi (Kieffer, 1913)

prolatus Lim, 2013

quadrifoveatus (Muesebeck, 1934)

ruficeps Kieffer, 1906

ruficrus Krombein, 1996

rufipedis Xu & He, 2006

taiwanus Terayama, 1997

telortis Lim & Lee, 2009

transvaalensis (Buysson, 1897)

ventralis Krombein, 1966

waterhousei (Kieffer, 1907)

xanthoneurus (Kieffer, 1911)

Omaloderus Walker, 1843

Original description— *Omaloderus* Walker 1843, 11: 188.

Type-species— *Omaloderus intrepidus* Walker, 1843.

Kind of designation— original monotypy.

Designator— Walker 1843, 11: 188.

Diagnosis (?sex)

- Body slender, flattened, almost smooth, black
- Head elongate, slightly wider than thorax
- Eye placed antero-laterally
- Ocellar triangle closed to vertex crest
- Antenna moniliform with 12(?) flagellomeres,
- Prothorax conical, large, posterior margin arched
- Mesonotum very short, 2x wider than long
- Parapsidal furrows well defined, parallel
- Scutellum small, inversely conical
- Metapectal-propodeal complex large
- Foretarsomere 5-segmented
- Metasoma with petiole short

Taxonomy. The original description of *Omaloderus* does not provide enough information to understand it accurately mostly because no illustration is provided and the characters described by Walker (1843) do not correspond to those more useful recognize the genus nowadays. *Omaloderus* was classified in Bethylini by Kieffer (1914), but Gordh & Móczár (1990) placed it in *incerta sedis* without any explanation. Two characters cited in the original description, such as the head wider thorax and the antennae moniliform lead us to believe that *Omaloderus intrepidus* and *Lytopsenella testaceicornis* could be one single species. However we were not able to find the type material to synonymized both species and genera.

Additionally, Walker (1843) cited the antennae as having 14 segments with uncertainty. If so, it would not be Bethylidae.

Starting point. This genus was treated in some detail by Walker (1843).

Distribution. Neotropical region, 01 species.

Hosts. Unknown.

Check list.
intrepidus Walker, 1843

Prosierola Kieffer, 1905

(Fig. 24 A–H)

Original description— Kieffer 1905 (in Kieffer & Marshall 1904–1906), 9: 243.
Type-species— *Epyris nasalis* Westwood, 1874.
Kind of designation— original monotypy.
Designator— Kieffer 1905 (in Kieffer & Marshall 1904–1906), 9: 243.

Diagnosis ♀ ♂

- Palpal formula 5:3
- Mandible with four sharpened apical teeth
- Notauli present or absent
- Mesoscutellar pits variable circular or semicircular, large or small
- Metapectal-propodeal complex with pair of conspicuous anterior pits
- Metapectal-propodeal complex with metaposnotal propodeal suture conspicuous
- Mesopleuron gibbous, angularly or roundly produced
- Forewing with four closed cells (R, 1Cu, C and 1M)
- Ventral carina of metasomal petiole present
- Paramere double, completely divided into dorsal and ventral arms (♂)

Taxonomy. The genus is easily recognized by the presence of a pair of conspicuous anterior pits on the metapectal-propodeal complex (Azevedo 2008b). This character is autapomorphic for the genus (Polaszek & Krombein 1994).

This is an infrequently captured bethylid genus, regardless of trap type or vegetation type (Azevedo 2008b).

Starting point. Azevedo (2008b) presented a synopsis of the genus including key, diagnosis and illustrations of its species.

Distribution. New World, 7 species.

Hosts. *Prosierola* attacks larvae of certain families of Lepidoptera, namely Olethreutidae (Muesebeck & Walkley 1951) and Pyralidae (Doutt 1973).

Check list

cubana Evans, 1964

flavicoxis (Kieffer, 1904)

nasalis (Westwood, 1874)

obliqua Evans, 1964

rotunda Schiffer & Azevedo, 2002

rufescens Evans, 1964

submersa Brues, 1933

Sierola Cameron, 1881

(Fig. 25 A–H)

Original description— Cameron 1881, 556.

Type-species— *Sierola testaceipes* Cameron, 1881.

Kind of designation— original monotypy.

Designator— Cameron 1881, 556.

Diagnosis ♀ ♂

- Notauli absent
- Metapectal-propodeal complex without median carina
- Metapectal-propodeal complex without metaposnotal propodeal suture

- Forewing with:
  - Five closed cells (R, 1Cu, C, 1M, and 2R1)
  - Pterostigma present and large
  - Prostigma present and large
  - 2R1 cell closed
  - 2R1 cell subtriangular and long
  - 1M cell present (areolet)

Taxonomy. The genus is easily recognized by having 1M cell present (areolet), and 2R1 cell subtriangular. However, the species of *Sierola* are apparently somewhat variable and not always easily distinguished one from another. The Hawaiian species have several morphological patterns, such as: basic form (species with carinate clypeus, and narrow mandibles), wedge-head (*S. laticeps*), viper-head (*S. distincta*), falcate-mandibles (*S. anthracina*), chopper-mandibles (*S. blackburni*), scissors-mandibles (*S. nigrescens*), and yellow-bodied (*S. kauaiensis*). Regarding the sexual dimorphism, the two sexes are often strikingly different, and the confusion would be inevitable result when one tries associating the males with their respective females.

Starting point. Fullaway (1920) presented descriptions of 171 new species including key, and illustrations of its species.

Distribution. Circum-pacific belt, 208 species (196 from Hawaii).

Hosts. The host associations of *Sierola* are poorly understood. However, Fullaway (1920) presented several records of members of this genus parasitizing lepidopterous larvae in concealed situations such as leafrollers. Fullaway (1920) presented records of 11 species attacking lepidopterous larvae, as follow: *Sierola aristoteliae* reared from larvae of *Aristotelia* species (Gelechiidae) infesting a *Gouldia* fruit (pg. 82); *S. batrachedrae* reared from *Batrachedra* species (Batrachedridae) (pg. 121); *S. capuana* reared from larva of *Capua cassia* and *Archips longiplicatus* (Tortricidae) (pg. 113); *S. cryptophlebiae* reared from larva of *Cryptophlebia illepida* (Tortricidae) (pg. 119); *S. epagogeana* reared from larva of *Epagoge infaustana* (Tortricidae) (pg. 135); *S. gracilariae* reared from *Gracilaria mabaella* (Gracillariidae) (pg. 118); *S. opogonae* reared from *Opogona* larva (Tineidae) (pg. 122); *S. perottetiae* reared from decaying wood of *Perottetia sandwicensis* (pg. 151); *S. philodoriae*

reared from larva of *Philodoria splendida* (Gracillariidae) (pg. 146); *S. pulchra* reared from leaf miner in *Urera* (pg. 97); *S. timberlakei* reared from larvae of *Batrachedra sophroniella* (Batrachedridae) (pg. 96).

Paul & Austin (2006) presented the information on the parasitoid complex associated with *E. postvittana* (Walker) and among these were found one *Sierola* species. According to Gordh (1998) there is report of *Sierola* attacking cecidomyiid fly larvae by Ashmead (1901), but this condition must be verified. Moreover, this author also indicated *Sierola ellingtoni* Gordh attacking pink bollworm, *Pectinophora gossypiella* (Saunders), a gelechiid moth endemic to Western Australia.

Gordh & Móczár (1990) and Tachikawa (1985a; 1985b) suggested that *Sierola* species attack lepidopterous larvae (Cosmopterygidae, Gelechiidae, Gracilariidae, Olethreutidae, Pyraustidae, Tineidae, and Tortricidae.

Check list

abusa Fullaway, 1920
acuta Fullaway, 1920
adamsoni Fullaway, 1935
adumbrata Fullaway, 1920
affinis Fullaway, 1920
agens Fullaway, 1920
amica Fullaway, 1920
anemophila Fullaway, 1920
angustata Fullaway, 1920
anthracina Fullaway, 1920
antipoda Ashmead, 1900
arida Fullaway, 1920
aristoteliae Fullaway, 1920
armata Fullaway, 1920
ashmeadi Gorbatovsky, 1995
aspera Fullaway, 1920
atra Fullaway, 1920
aucta Fullaway, 1920
batrachedrae Fullaway, 1920

bella Fullaway, 1920
berryae Ward, 2013
bicolor Fullaway, 1920
blackburni Fullaway, 1920
brevicauda Fullaway, 1920
breviceps Fullaway, 1920
brevicornis Fullaway, 1920
bridwelli Fullaway, 1920
brunnea Fullaway, 1920
brunneipennis Fullaway, 1920
brunneipes Fullaway, 1920
brunneiventris Fullaway, 1920
bryani Fullaway, 1920
callida Fullaway, 1920
capuana Fullaway, 1920
carinata Fullaway, 1920
celeris Fullaway, 1920
collaris Ashmead, 1901
compacta Fullaway, 1920
conspicua Fullaway, 1920
cookei Fullaway, 1935
croceipes Fullaway, 1920
cryptophlebiae Fullaway, 1920
curiosa Fullaway, 1920
curvignatha Fullaway, 1920
depressa Fullaway, 1920
depressela Fullaway, 1920
dichroma Perkins, 1910
distincta Fullaway, 1920
distingueda Fullaway, 1920
ehrorni Fullaway, 1920
ellingtoni Gordh, 1988
emarginata Fullaway, 1920

epagogeana Fullaway, 1920
eucrena Fullaway, 1920
flavicornis Fullaway, 1920
flavipennis Fullaway, 1920
flavipes Fullaway, 1920
flavocollaris Ashmead, 1901
fossulata Fullaway, 1920
freycinetiae Fullaway, 1935
fuliginosa Fullaway, 1920
fusca Fullaway, 1920
fuscipennis Fullaway, 1920
fuscipes Fullaway, 1920
giffardi Fullaway, 1920
gilbertae Ward, 2013
glabra Fullaway, 1920
gracilariae Fullaway, 1920
gracilis Fullaway, 1920
gracillima Fullaway, 1920
gregoryi Fullaway, 1935
hastata Sorg, 1988
hillebrandi Fullaway, 1920
hirticeps Fullaway, 1920
hissuta Fullaway, 1920
hivaoaensis Fullaway, 1935
holomelaena Fullaway, 1920
humilis Fullaway, 1920
illingworthi Fullaway, 1920
imparata Fullaway, 1920
incita Fullaway, 1920
indecora Fullaway, 1920
indra Terayama, 2004
izanami Terayama, 2006
kaala Fullaway, 1920

kaalensis Fullaway, 1920
kaduana Fullaway, 1920
kalihiensis Fullaway, 1920
kauaiensis Ashmead, 1901
kauensis Fullaway, 1920
kaumuohona Fullaway, 1920
kilauea Fullaway, 1920
koa Fullaway, 1920
koebelei Fullaway, 1920
konana Fullaway, 1920
koolauensis Fullaway, 1920
lacessita Fullaway, 1920
langfordi Fullaway, 1920
lanihuliana Fullaway, 1920
larifuga Evans, 1978
lata Fullaway, 1920
laticeps Fullaway, 1920
lebronnecii Fullaway, 1935
leeuwinensis Turner, 1915
lepida Fullaway, 1920
leuconeura Cameron, 1886
levigata Fullaway, 1920
levis Fullaway, 1920
localis Fullaway, 1920
longicaudata Fullaway, 1920
longiceps Fullaway, 1920
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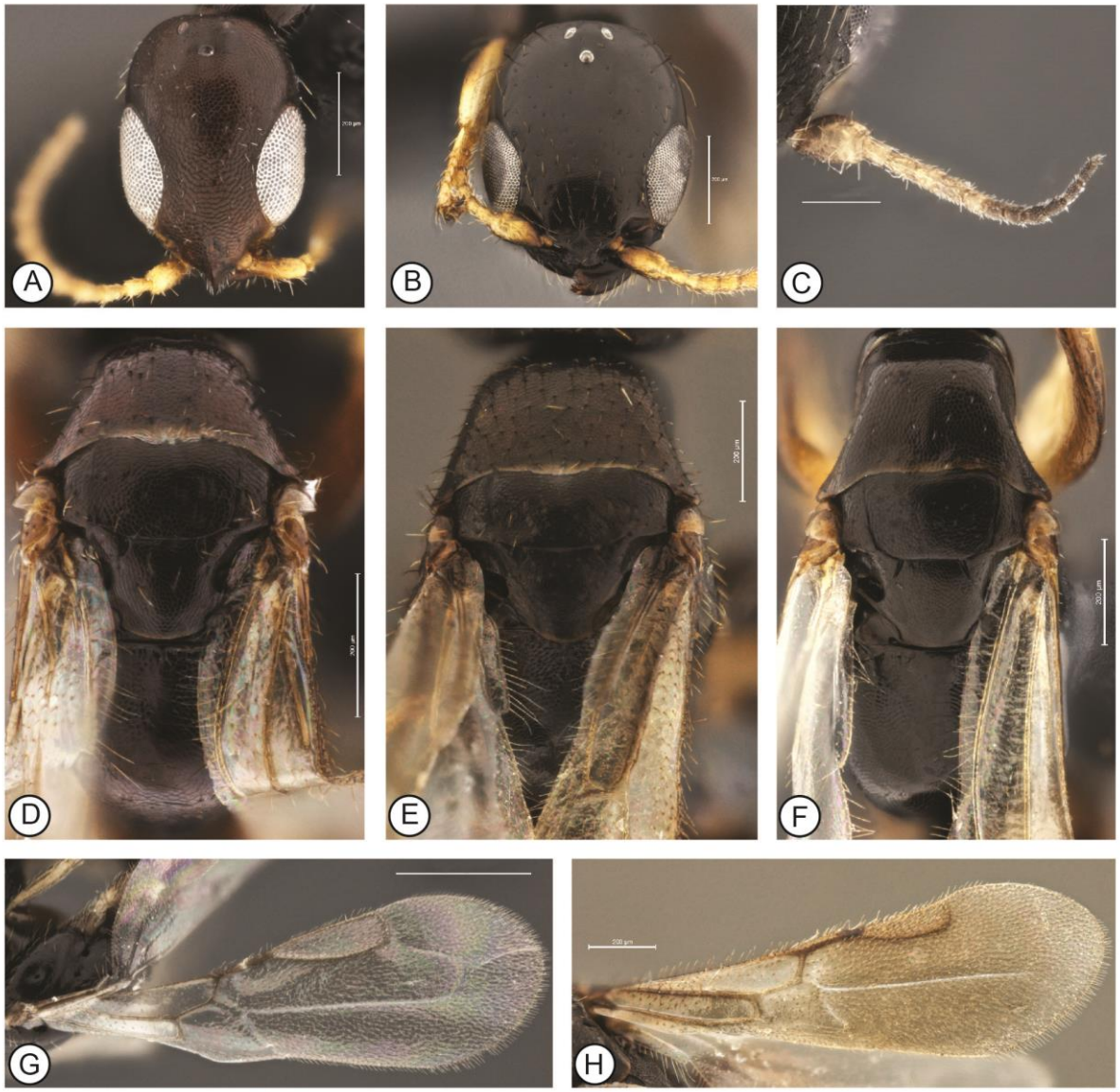
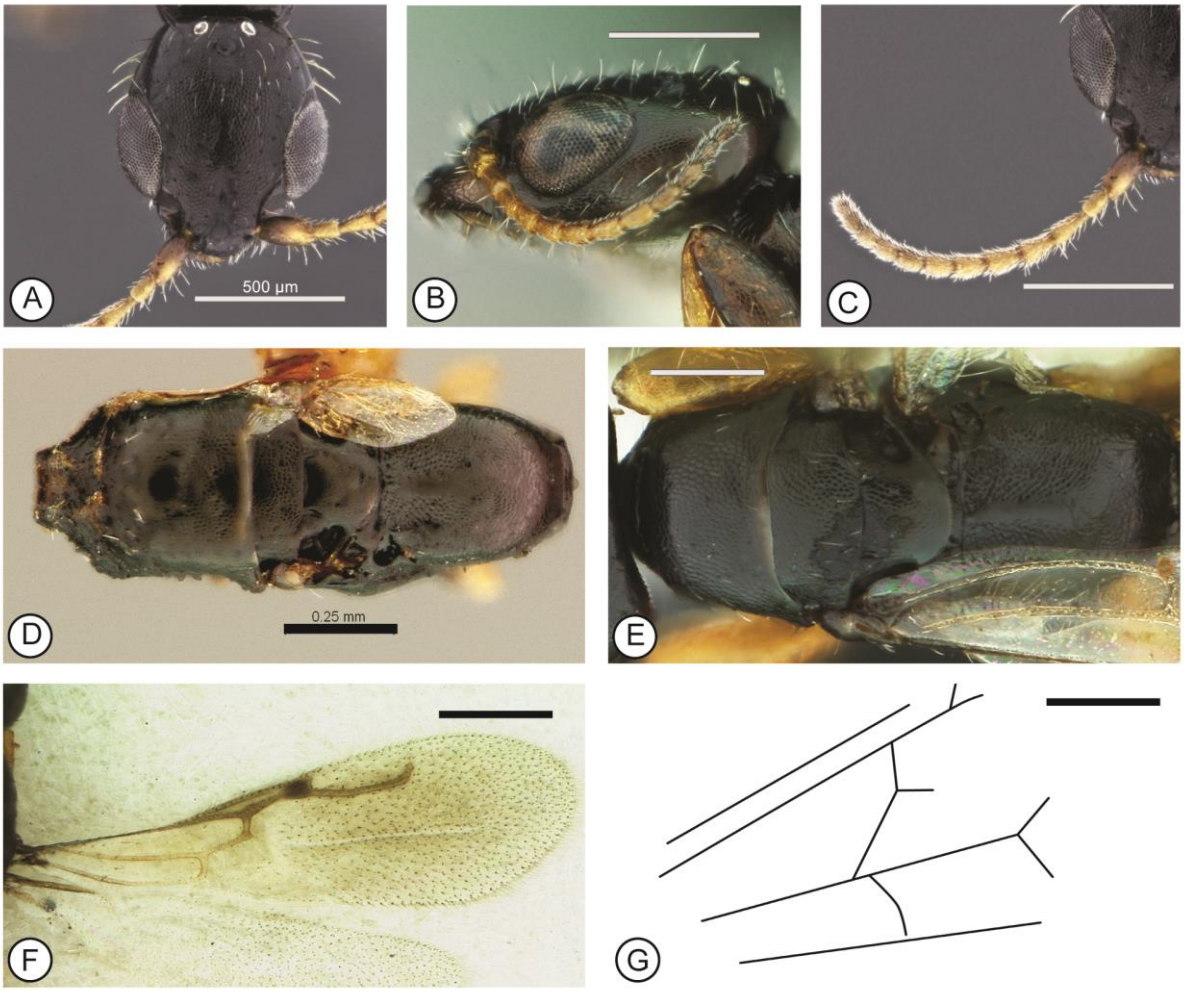


FIGURE 18. *Afrobethylus* Ramos &Azevedo, 2016. A–B. Head, dorsal view; C. Antenna, dorsal view; D–F. Mesosoma, dorsal view; G–H. Right forewing. (Scale bar = 100 µm).



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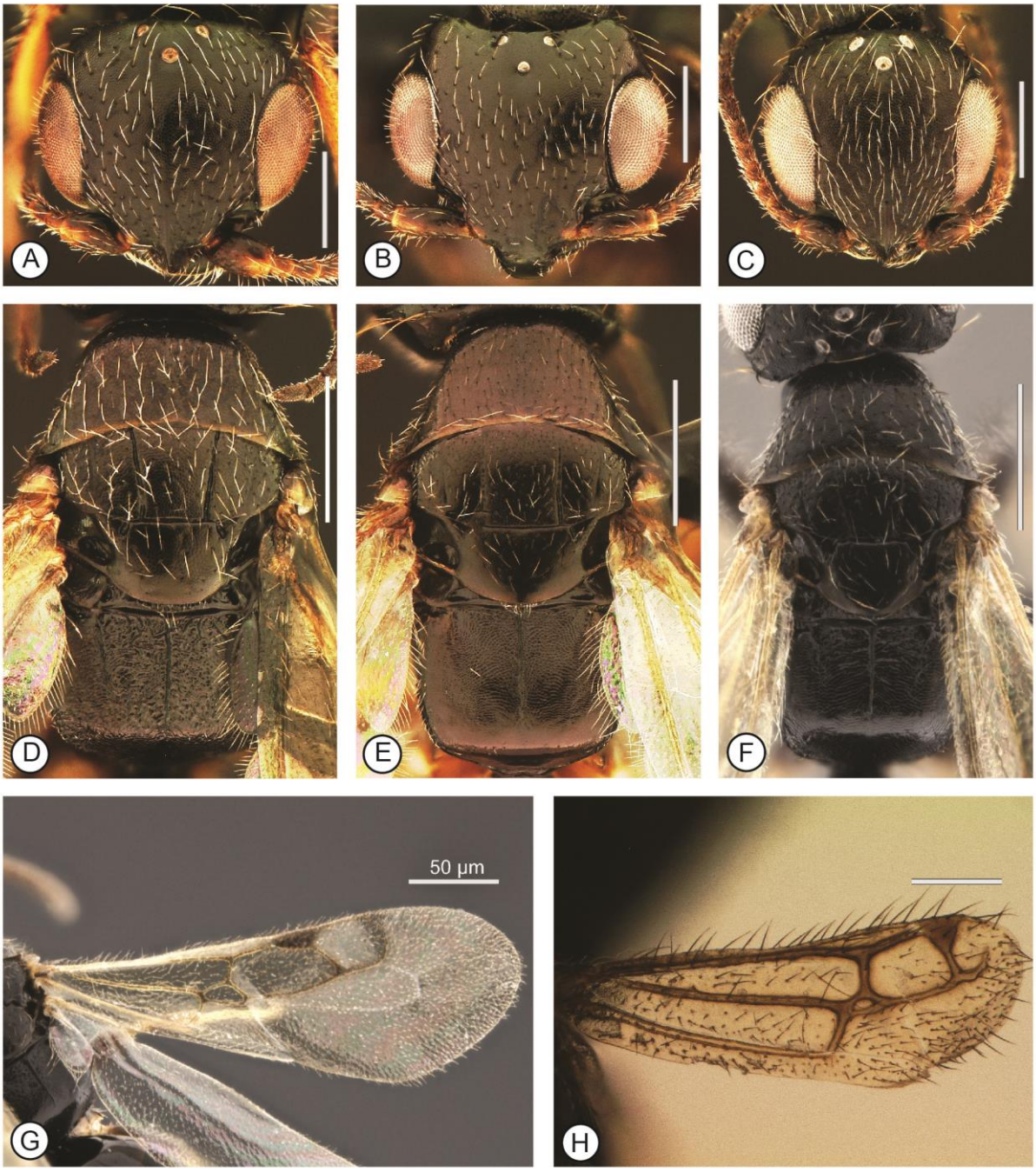

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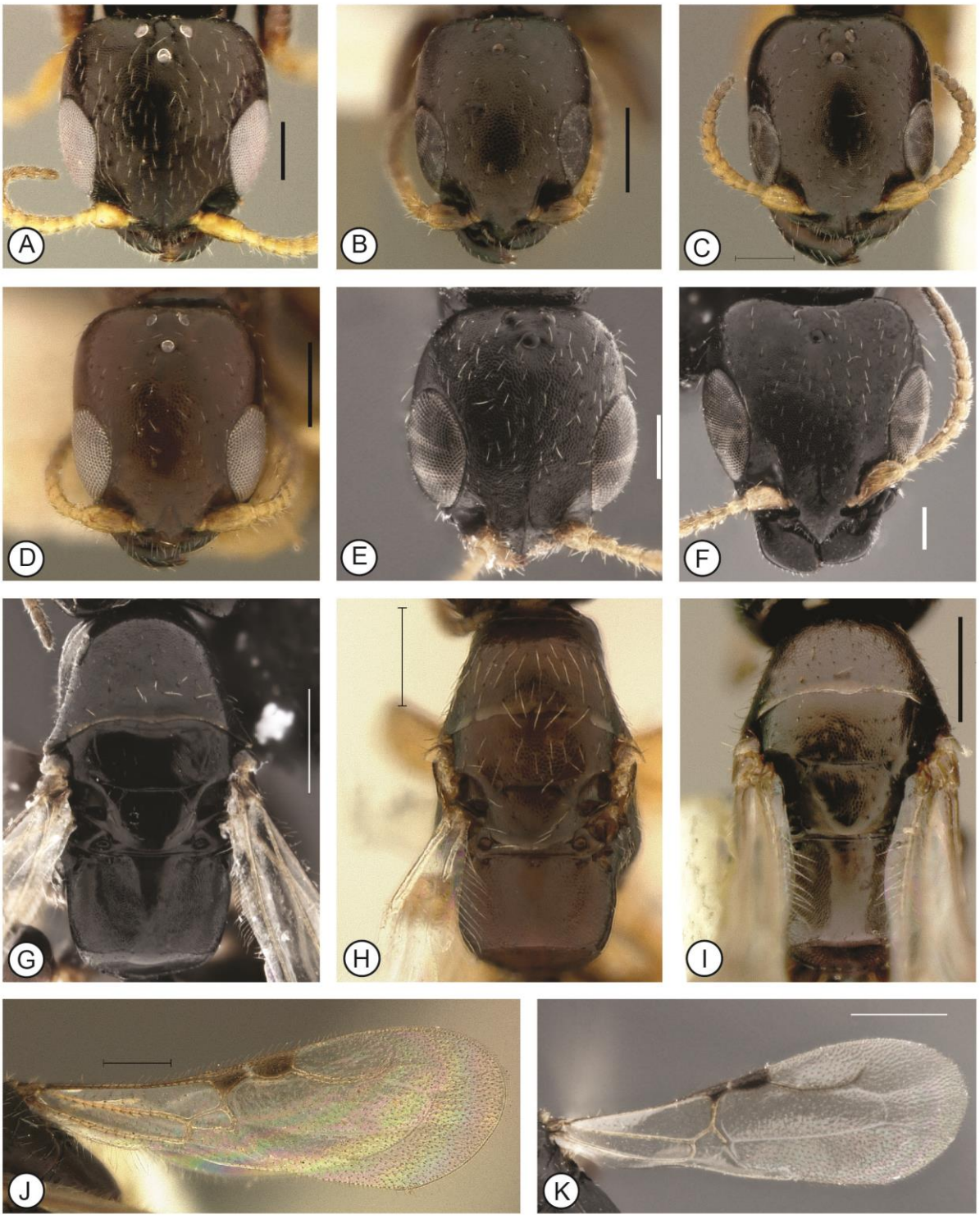

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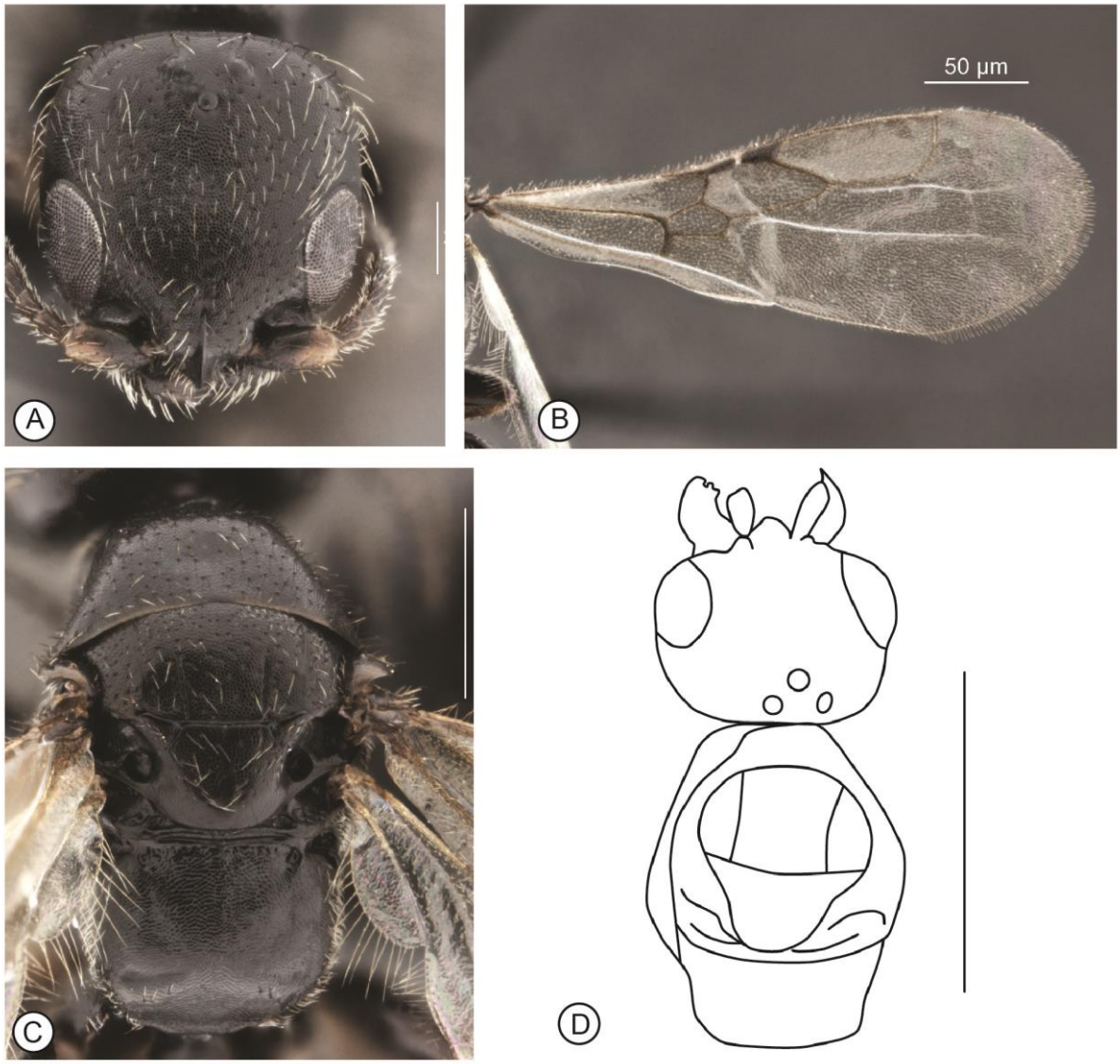

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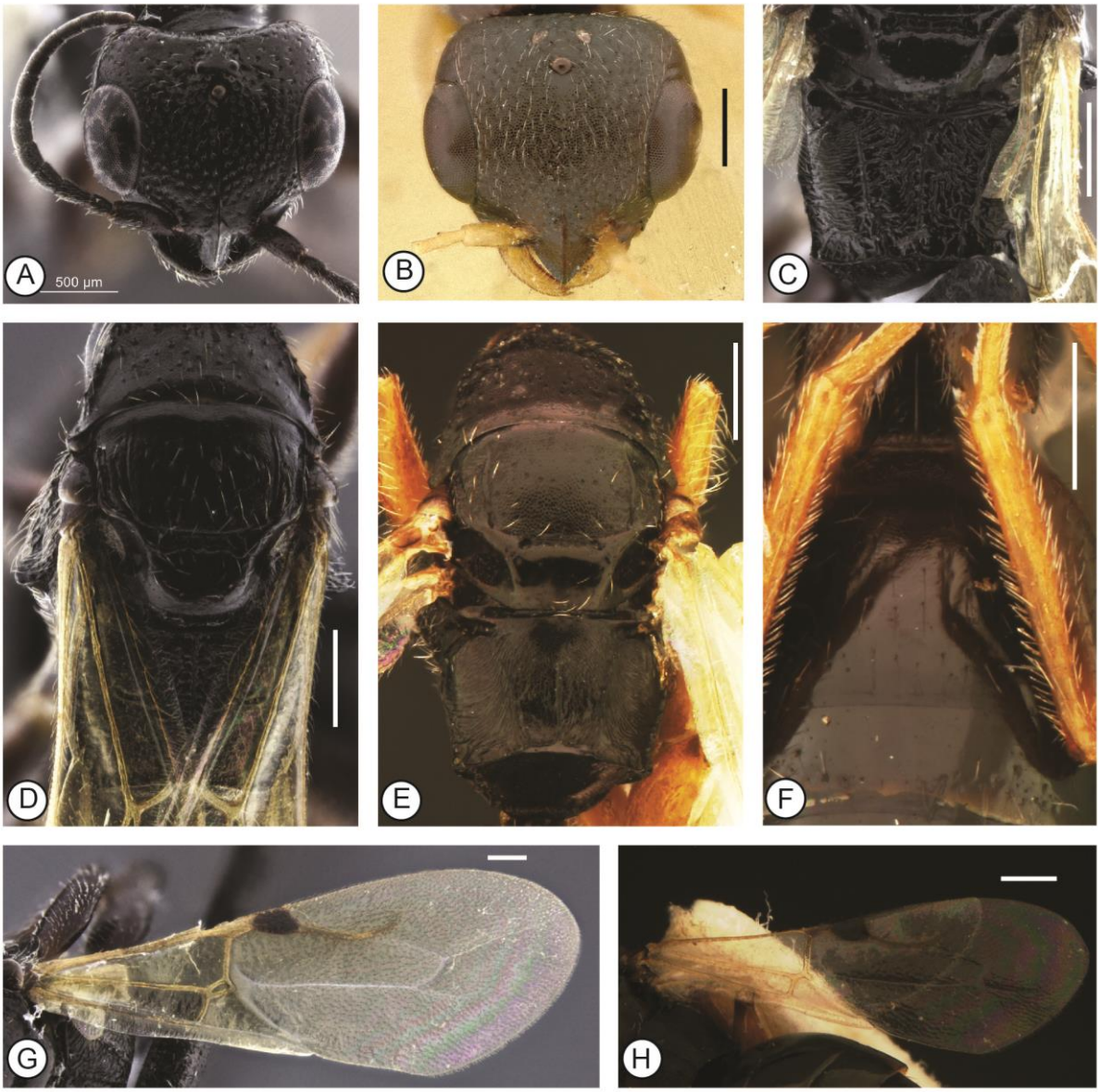

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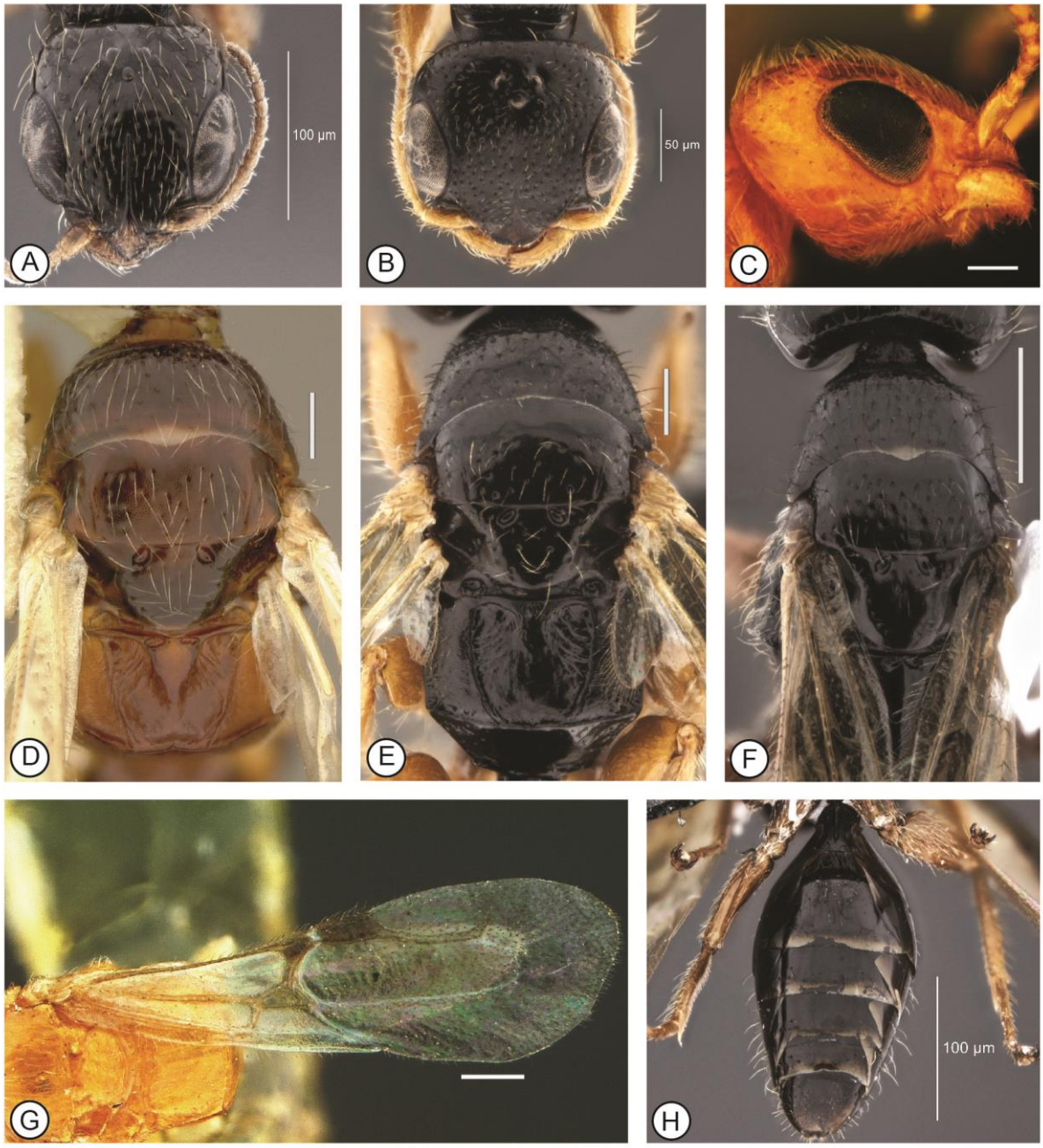

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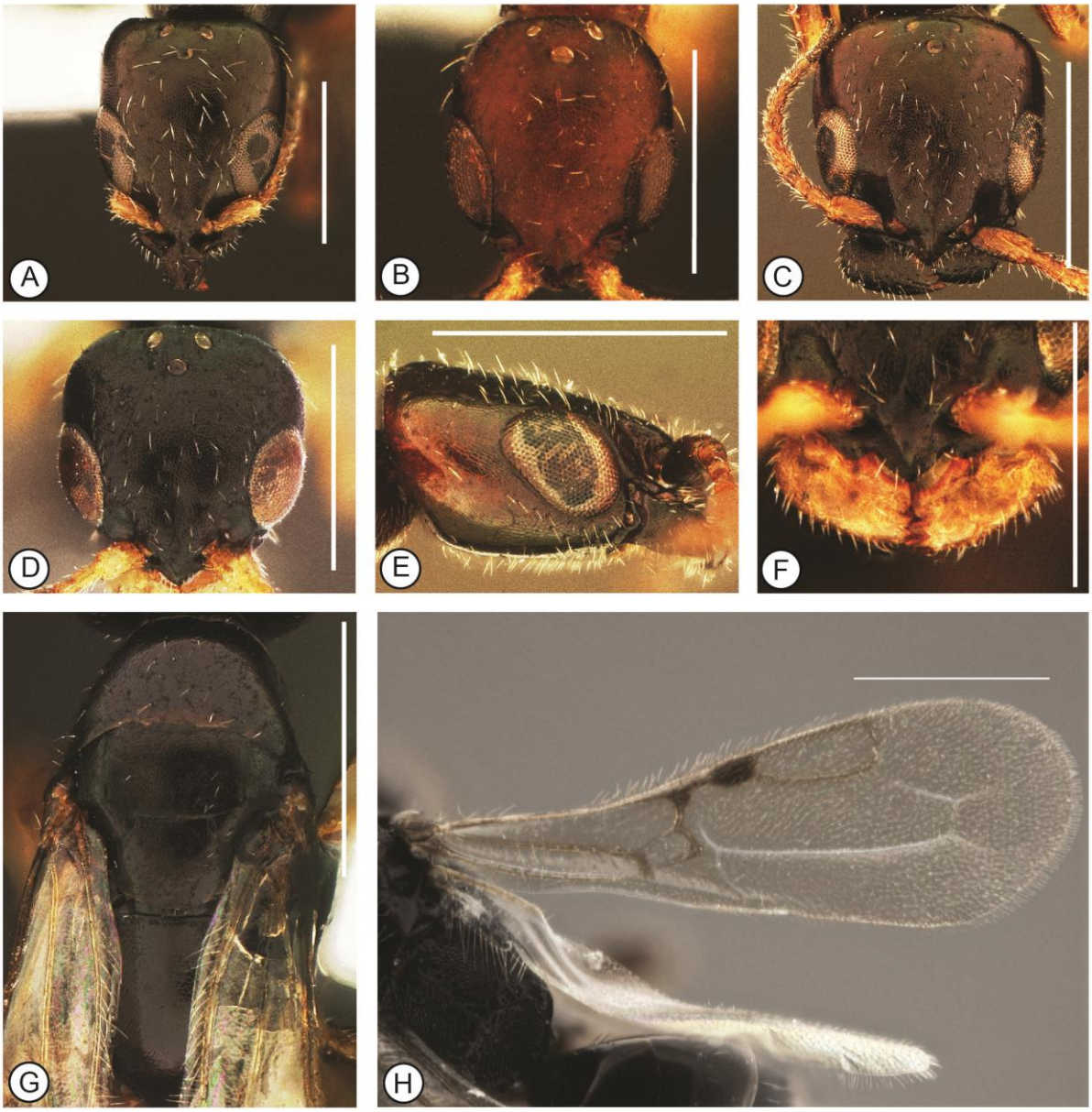

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